

Received: 1 July 2016 | Revised: 16 August 2016 | Accepted: 20 August 2016

DOI: 10.1002/ece3.2469

REVIEW

WILEY *Ecology and Evolution* 

Emissions of methane from northern peatlands: a review of management impacts and implications for future management options

Mohamed Abdalla¹ | Astley Hastings¹ | Jaak Truu² | Mikk Espenberg² |
Ülo Mander^{2,3} | Pete Smith¹

¹Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen, UK

²Department of Geography, Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia

³Hydrosystems and Bioprocesses Research Unit, National Research Institute of Science and Technology for Environment and Agriculture (Irstea), Antony Cedex, France

Correspondence

Mohamed Abdalla, Institute of Biological and Environmental Sciences, School of Biological Sciences, University of Aberdeen, Aberdeen, UK.
Email: mabdalla@abdn.ac.uk

Abstract

Northern peatlands constitute a significant source of atmospheric methane (CH₄). However, management of undisturbed peatlands, as well as the restoration of disturbed peatlands, will alter the exchange of CH₄ with the atmosphere. The aim of this systematic review and meta-analysis was to collate and analyze published studies to improve our understanding of the factors that control CH₄ emissions and the impacts of management on the gas flux from northern (latitude 40° to 70°N) peatlands. The analysis includes a total of 87 studies reporting measurements of CH₄ emissions taken at 186 sites covering different countries, peatland types, and management systems. Results show that CH₄ emissions from natural northern peatlands are highly variable with a 95% CI of 7.6–15.7 g C m⁻² year⁻¹ for the mean and 3.3–6.3 g C m⁻² year⁻¹ for the median. The overall annual average (mean ± SD) is 12 ± 21 g C m⁻² year⁻¹ with the highest emissions from fen ecosystems. Methane emissions from natural peatlands are mainly controlled by water table (WT) depth, plant community composition, and soil pH. Although mean annual air temperature is not a good predictor of CH₄ emissions by itself, the interaction between temperature, plant community cover, WT depth, and soil pH is important. According to short-term forecasts of climate change, these complex interactions will be the main determinant of CH₄ emissions from northern peatlands. Drainage significantly ($p < .05$) reduces CH₄ emissions to the atmosphere, on average by 84%. Restoration of drained peatlands by rewetting or vegetation/rewetting increases CH₄ emissions on average by 46% compared to the original premanagement CH₄ fluxes. However, to fully evaluate the net effect of management practice on the greenhouse gas balance from high latitude peatlands, both net ecosystem exchange (NEE) and carbon exports need to be considered.

KEYWORDS

bog, drainage, fen, methane emissions, natural peatlands, restoration

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

1 | INTRODUCTION

The concentration of methane (CH_4) in the atmosphere has increased from 722 ppb during the pre-industrial period to 1,819 ppb in 2012, due to increased anthropogenic emissions (Ciais et al., 2013; Whalen, 2005). Methane is the second most important greenhouse gas (GHG) after carbon dioxide (CO_2). Although it contributes less than 0.5% of the atmospheric carbon (C) gas concentration, it constitutes about 20% of the global radiative forcing (IPCC, 2013). This is because CH_4 has a much stronger radiative forcing (i.e., is 34 times stronger than CO_2) (IPCC, 2013). For an emission pulse of similar mass of C, CH_4 creates a powerful immediate radiative forcing at the start, but due to its shorter atmospheric lifetime, this declines faster than for CO_2 (IPCC, 2013).

Globally, CH_4 emissions are about 500–600 Tg CH_4 per year (Bruhwiler et al., 2014; Kirschke et al., 2013). Approximately, 40% of these emissions are from natural sources, mainly wetlands, while the rest (60%) are due to microbial emissions in rice agriculture, livestock grazing and waste, biomass burning, and fossil fuel (Denman et al., 2007). Northern peatlands (i.e., latitude 40° – 70°N) emit about 36 Tg CH_4 -C per year (Zhuang et al., 2006), which is equivalent to 11% of the total CH_4 emissions (Wuebbles & Hayhoe, 2002).

In wetland soils, CH_4 is produced in the anaerobic zones of submerged soils by methanogens, is oxidized to CO_2 by methanotrophs in the aerobic zones, and is emitted to the atmosphere when the balance between the production and consumption is positive (Le Mer & Rodger, 2001). Peat soil accumulation derives from a positive water balance and a water table (WT) close to the soil surface, which results in anaerobic conditions preserving organic material (Belyea & Clymo, 2001; Lai, 2009), and that is also a prerequisite for methanogenesis, the terminal step of anaerobic organic matter mineralization (Hou, Wang, Chen, & Patrick, 2000; Yavitt & Williams, 2000). Both the CH_4 directly produced in the peat soil and atmospheric CH_4 can be oxidized as an energy source, or used for biosynthesis by methanotrophs (Conrad, 1996; Hanson & Hanson, 1996).

In a recent review, Turetsky et al. (2014) concluded that the CH_4 flux from fens is more sensitive to the vegetation type present and less sensitive to soil temperature than fluxes from bog or swamp ecosystems. Water table depth and temperature are the major controls on CH_4 emissions from natural bogs and swamps, but other processes like vascular transport in plants could partially override the effect of these controls in other wetland types, for example, fens. Other previous studies have identified many environmental factors that exert significant control over CH_4 emissions from peatlands, including microtopography and plant species composition (Bubier, Moore, & Roulet, 1993; Nilsson et al., 2001), temperature (Ding & Cai, 2007; Granberg, Mikkilä, Sundh, Svensson, & Nilsson, 1997; Saarnio et al., 1998), WT depth and soil moisture (Frenzel & Karofeld, 2000; Granberg et al., 1997; Hargreaves & Fowler, 1998; Liblik, Moore, Bubier, & Robinson, 1997; Moore & Knowles, 1989; Sundh, Mikkilä, Nilsson, & Svensson, 1995; Yang et al., 2006), atmospheric N deposition (Bodelier & Laanbroek, 2004; Granberg, Sundh, Svensson, & Nilsson, 2001), pH

(Hutsch, 1998; Singh, Singh, & Kashyap, 1999), and availability and quality of substrate (Granberg et al., 1997; Joabsson, Christensen, & Walle'n, 1999).

Methane can also be released to the atmosphere in bubbles (ebullition) which take place when there are gas pockets in the waterlogged soil, or the dispersal of the gas is prevented by a layer of dense peat or ice (Baird, Beckwith, Waldron, & Waddington, 2004; Tokida et al., 2007). Air pressure has an important role in establishing the timing and quantity of CH_4 ebullition (Tokida et al., 2007). In the Aapa mires (fens), CH_4 confined under ice layers can be released in the spring thaw, representing about 11% of the annual emissions (Tokida et al., 2007). In these situations, large quantities of CH_4 ($>40 \text{ g CH}_4 \text{ m}^{-2}$) may be released to the atmosphere over periods of minutes to hours (Glaser et al., 2004; Rosenberry, Glaser, Siegel, & Weeks, 2003), where CH_4 bubbles are transported through the peat too fast to allow oxidation to occur. Methane can also be released to the atmosphere via vascular plants (Joabsson et al., 1999; King, Reeburgh, & Regli, 1998). Under anoxic conditions, vascular plants in wetlands may transport O_2 through specialized, aerenchymatous tissues, by which CH_4 can also be released to the atmosphere (Joabsson et al., 1999). The exchange of O_2 and CH_4 through vascular plants between the anoxic zone and the atmosphere may have contrasting effects on CH_4 emissions in northern peatlands. Methane production by methanogenic archaea could be inhibited by the transport of O_2 into otherwise anaerobic layers, or oxidized due to release of O_2 into the rhizosphere. Due to this bypass release of CH_4 , the net emission to the atmosphere tends to increase when aerenchymatous vascular plants are present (Joabsson et al., 1999). Further, CH_4 has low solubility in water (23–40 mg/L at 0–20°C) and could escape through sediment into the atmosphere by either diffusion or ebullition. The gas could be transported through vascular plants (Joabsson et al., 1999) or diffused slowly upward through peat soils where the methanotrophic bacteria are able to oxidize it to CO_2 . Analyzing a large UK data set on CH_4 emissions from soils, Levy et al. (2012) found that where plant species composition data (percentage cover of aerenchymatous plant species) were available, this provided the highest explanatory power of CH_4 fluxes to the atmosphere.

Northern peatlands represent a crucial ecosystem for regional GHG budgets because they store large amounts of C (Loisel et al., 2014). However, the ratio between decomposition and conservation of the C depends on the vegetation types present, for example, Sphagnum mosses are more resistant to decomposition compared to sedges and other vascular plants and thereby retain more C over time (Rydin & Jeglum, 2006). Peatlands can be divided into two main categories, depending on their hydrology and nutrient status. These are (1) ombrotrophic peatlands (bogs) which receive water and nutrients from atmospheric deposition and thus are acidic and poor in nutrients and (2) minerotrophic peatlands (fens) which receive water and nutrients from the surrounding mineral soils in the catchment. Nutrient status in fens varies from close to ombrotrophic nutrient-poor conditions to mesotrophic/eutrophic conditions, mainly controlled by the ratio between the peatland and mineral soil area, and the mineral

nutrient status in that catchment (Clymo, 1983). Differences between the peatland types are also reflected in vegetation composition, primary production, organic matter decomposition, and C gas emissions (Clymo, 1983; Nilsson et al., 2001). Peatlands are also classified into aquatic, forb, graminoid, lichen, moss, nonvegetated, shrub, and treed based on the general form of the vegetation cover, rather than on species (Adams et al., 1997).

Management of peatlands, through, for example, changes in land use, drainage, and cultivation of natural peatlands and application of N fertilizer disturb methanogenic archaea (Reeburg, Whalen, & Alperin, 1993) and methanotrophic bacteria (Seghers et al., 2003; Tate et al., 2007), leading to peatlands becoming a weak CH₄ sink (Castaldi, Ermice, & Strumia, 2006; Tate et al., 2007). Large areas of northern peatland have been drained and used for agriculture, forestry, and peat extraction (Laine, Vasander, & Laiho, 1995). Peatlands are drained to lower the WT away from the surface and this has profound impacts on the functioning of the peatlands. Lowering WT by drainage results in changing biological, chemical, and physical characteristics of the soils, enhancing soil aeration (Hillman, Gerbemedhin, & Warner, 1992; Prevost, Belleau, & Plamondon, 1997) and increasing soil temperatures (Kirschbaum, 1995), thereby reducing CH₄ emissions (Nykänen, Alm, Silvola, Tolonen, & Martikainen, 1998; Von Arnold, Nilsson, Hanell, Weslien, & Klemedtsson, 2005; Von Arnold, Weslien, Nilsson, Svensson, & Klemedtsson, 2005). On the other hand, restoration practices aim to re-establish the conditions that encourage peat accumulation (Kimmel & Mander, 2010; Vasander et al., 2003). They include techniques to raise the WT and re-establish vegetation cover that could enhance the waterlogged environment and enable peat accumulation to be established (Worrall et al., 2011).

Wetland restoration is one method with which northern countries could aim to meet their GHG targets under the Kyoto Protocol (Bain, Hornsey, Bongiorno, & Jeffries, 2012). In contrast to drainage, restoration raises the WT, increases water saturation, and thus may increase CH₄ emissions (Saarino, Winiwarer, & Leitao, 2009). The WT level controls the balance between CH₄ and CO₂ emissions and the rate of CH₄ emissions to the atmosphere is therefore very sensitive to WT depth (Price & Ketcheson, 2009; Sirin & Laine, 2008). The most prevalent restoration method is drain blocking, which could restore the WT to its initial state (Holden et al., 2007), or raising the WT by gully and ditch blocking (Evans, Monteith, & Cooper, 2005). Other restoration methods include planting and reseedling of bare surfaces, or re-establishment of natural peatland vegetation, which is important, as vegetation is a major factor in peat formation (Petrone, Price, Waddington, & von Waldow, 2004; Vitt, 2006).

Predicted changes in climate, including rising temperatures, changes in the amount, intensity, and seasonal distribution of precipitation and amount of snow fall and cover (IPCC, 2013), could affect the dynamics of hydrology in northern peatlands and could increase methane production (FAO, 2008). Additionally, the exploitation of peatlands for agriculture, energy, and horticulture under intensive management also greatly influences the rate of mineralization (CO₂ emissions) (Laine et al., 1995). Higher CH₄ emissions could lead to a positive feedback on climate change and thereby

further disturbance of peatland C stocks (Friedlingstein et al., 2006). It is suggested that climate change reduces the capacity of northern peatlands to absorb atmospheric carbon dioxide (Wu & Roulet, 2014) and this depends on how management, and the interaction with climate change, will affect CH₄ emissions. The aim of this systematic review and meta-analysis was to collate and analyze published studies to improve our understanding of the factors that control CH₄ emissions and the impacts of management on the gas flux from northern peatlands. The specific hypotheses that we tested were as follows: (1) Methane emission is mainly controlled by WT, plant community, temperature, and pH; (2) management, especially drainage and restoration, significantly affects CH₄ emissions; and (3) climate change will significantly reduce the capacity of northern peatlands to absorb the atmospheric C.

2 | MATERIALS AND METHODS

2.1 | Data collection

To locate all papers that have reported CH₄ emissions from northern peatlands, we performed a comprehensive search on the Web of Science database (accessed between January 2013 and July 2016) using the keywords: pristine peatlands, methane emissions, drainage, restoration, fens, bogs, mire, and northern peatlands. In an attempt to gain a comprehensive coverage, we also checked all references in the papers found in the Web of Science search. Only studies which covered at least one growing season and measured at weekly or more frequent intervals were selected. These searches resulted in 87 studies reporting measurements of CH₄ emissions taken at 186 sites covering different countries, peatland types, and management systems (Fig. 1). To indicate the direction of the methane flux, we used the atmospheric science sign convention, that is, a negative sign represents uptake of CH₄ gas by the ecosystem. In cases where a site has several years of flux data, the average flux of these years was used. If the flux values covered the growing season only, we estimated the annual flux values based on a previously used factor, generated from studies with full annual measurements coverage, whereby winter fluxes were estimated to constitute 15% of the annual CH₄ fluxes (Maljanen et al., 2010; Saarino et al., 2007). All CH₄ flux values were converted to g C m⁻² year⁻¹. The overall CH₄ flux average \pm SD (g C m⁻² year⁻¹) for "natural peatlands" was based on site averages reported in each publication and did not account for the variation between years at a single site. Some studies are repeated in more than one table because they include more than one site of different management systems.

For the studies included in this meta-analysis, CH₄ fluxes were measured using different methods which may differ in their ability to capture ebullition fluxes. These are manual chamber measurements, autochambers, and eddy covariance flux towers. Also, different methods were used to measure soil pH, for example, using pH probe/meter in deionized water or 0.01 M CaCl₂ in 1:1 and 1:2 or 1:5 (v:v) soils: solution ratios. We assumed the pH results to be equivalent and, where a range of values were reported, we took the mean. Where air

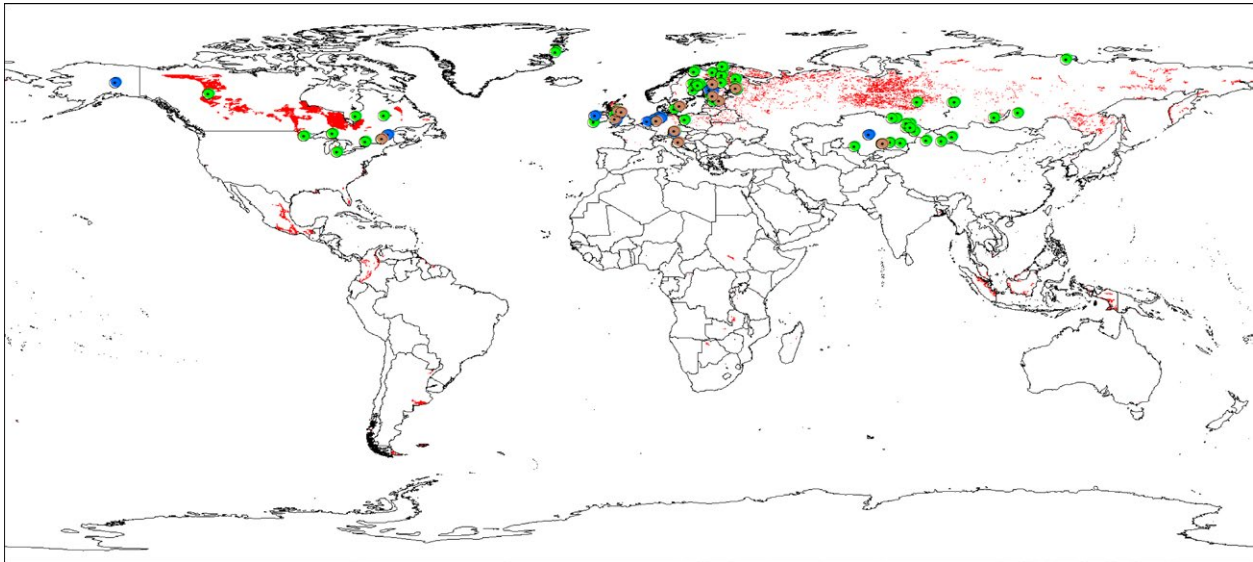


FIGURE 1 World map showing the experimental sites included in this study, across the northern peatlands. Symbols: Green = pristine, brown = drained, blue = restored; the red areas indicate histosols

temperature was reported, we used the mean annual temperature in degree Celsius ($^{\circ}\text{C}$) as variations between years were minor. The WT was reported relative to the surface in centimeters (cm) and we used the convention of negative values representing distance below the surface. Where a range of water levels was reported over the study, we used the mean value in the meta-analysis. In this review, we have adopted the classification of fens/bogs, for consistency, as most of the sites included were classified into fen or bog. From the descriptions of the sites in each paper used in this study, we assigned a peatland type of either fen or bog or wooded fen and bog.

2.2 | Data analysis

We used Minitab 16 (Minitab Inc., State College, PA, USA) and R version 3.3.0 (R Development Core Team, 2016) for data exploration, conditioning, and analysis. We split the literature studies into three groups for analysis: natural, drained, and restored. We used different analytical procedures for each group appropriate for the available published data.

2.2.1 | Natural peatlands

The data collected from natural peatlands covered 56 studies and 108 sites. The predictive variables available to test the response variable of annual methane flux were as follows: latitude, longitude, duration of measurement, mean annual air temperature (T), mean pH (pH), and mean WT as covariates and bog, fen, and woodland as random factors. Data exploration using matrix plots determined that latitude was colinear with mean annual air temperature as were mean pH and WT depth with their maximum and minimum values and these were excluded from the analysis. Annual precipitation, evapotranspiration, and water flow through were not available for most studies so observed WT depth was used

as the explanatory variable relating to both water supply and the oxidation status. Normality in flux and residual was tested and the flux was log-transformed. A one-way ANOVA test was performed to test whether there was a significant difference in emissions between bog, fen, and wooded peatlands. Next a linear mixed-effects model (LMM) was applied to test annual methane flux relationships with environmental variables and type of peatland using the “lmer” method (version 1.1–12) (Bates, Mächler, Bolker, & Walker, 2014), while p -values were calculated in order to confirm the significance of the relationships using the lmerTest package version 2.0–30 (Kuznetsova, Brockhoff, & Bojesen Christensen, 2013) in R version 3.3.0 (R Development Core Team, 2016). The package “piecewiseSEM” version 1.1.3 (Lefcheck and Jonathan, 2016) was used to calculate values for explained variation for obtained linear mixed-effects models. Not all variables were available at all sites with pH being available for the least, so the LMM was performed on samples that had pH values ($n = 36$) and then repeated on samples without the variable “pH” ($n = 76$). Then, package “missMDA” version 1.10 (Josse & Husson, 2016) was applied to impute missing data values, resulting in 108 samples to which the LMM was applied for all samples and all variables. Multiple linear regression analysis was applied to estimate the variation explained by two environmental variables.

The package “akima” version 0.5–12 was used to create interpolated contour plots (Akima & Gebhardt, 2015) of pairs of the environmental parameters as x and y with annual CH_4 emissions as the z variable. This was made for both the available study data and the imputed data to verify that the data trends were similar and the imputed values are valid. As WT and peatland type explained 42% of the variability, we performed linear regressions of these variables against the log-transformed annual CH_4 flux, with and without identified outliers. Then, we estimated the regression model of annual CH_4 flux and mean annual water level by nonlinear least squares, using the R function “nls.”

2.2.2 | Drained peatlands

The data were tested, using paired *t*-tests on all paired sites where both natural (*n* = 42) and artificially drained (*n* = 61) (i.e., lower water table for using in agriculture, forestry or mining) peatlands had CH₄ emission measurements.

In addition, a *t*-test was performed to see whether there was a significant difference between drained fens (*n* = 26) and drained bogs (*n* = 35). The effects of different land use systems/vegetation cover (cropland [*n* = 4], grassland [*n* = 7], and woods [*n* = 29]) on drained peatland methane emissions were also tested using one-way ANOVA.

2.2.3 | Restored peatlands

The impacts of restoration system on CH₄ emissions from peatlands were investigated. The management systems tested using paired *t*-test were as follows: rewetting (*n* = 16), and restoring by vegetation and rewetting (*n* = 16).

3 | RESULTS

3.1 | Methane emissions from northern natural peatlands

Our results show that natural northern peatland (pristine) sites are important sources for CH₄ emissions to the atmosphere (Table 1) with an overall average annual flux (mean ± SD) covering all sites, vegetation, and locations being 12 ± 21 g C m⁻² year⁻¹. The median is 4.3 g C m⁻² year⁻¹. However, emissions between the sites were highly variable with a 95% CI of 7.6–15.7 g C m⁻² year⁻¹ for the mean and 3.3–6.3 g C m⁻² year⁻¹ for the median. A *t*-test (*t* = -1.99) shows that CH₄ emissions from the fen sites (*n* = 59) mean 15.4 g C m⁻² year⁻¹ are significantly higher (*p* = .05) than those from the bog sites (*n* = 49) 7.1 g C m⁻² year⁻¹ (Fig. 2). A linear regression between log CH₄ flux and mean WT depth for different peatland types showed significant correlations for bog (*n* = 87, *r*² = 0.54, *p* < 0.01) and fen (*n* = 45, *r*² = 0.13, *p* < 0.01), but not for wooded fen and bog (*n* = 7, *r*² = 0.36, *p* = 0.09) (Fig. 3A). When four outliers were removed, the correlation was significant for fen (*n* = 43, *r*² = .22, *p* < .001) but not for bog (*n* = 33, *r*² = .36, *p* = .8) or wooded fen and bog (*n* = 7, *r*² = .36, *p* = .09) (Fig. 3B). The significant correlation between log CH₄ flux and mean WT depth (Fig. 4) suggested an exponential model which was tested by a nonlinear regression and resulted in the following relationship:

$$\text{CH}_4 = 32.462 \times \exp^{(0.08 \times \text{WT})} (n=87, r^2=0.54, p<0.01)$$

[Correction added on 24 September 2016, equations in the Results section were incorrect and have been corrected in this version.]

The contour plots in Fig. 5A show a trend toward higher CH₄ emissions with a high water table and high pH and with lower temperature, peaking at a mean annual air temperature around 2°C. The LMM results with samples that had a pH value (30 observations/samples) showed that pH is a statistically significant factor (*p* = .04). The proportion of

variance explained by the fixed factor(s) alone is 34% of CH₄ flux variation. The proportion of variance explained by both the fixed and random factors is 53%. The LMM results with samples in cases when the variable "pH" was omitted, where the number of observations is 76, shows that "peatland type" and WT are statistically important factors (*p* < .05 & *p* < .01, respectively). The proportion of variance explained by the fixed factor(s) alone is 19% of CH₄ flux variation. The proportion of variance explained by both the fixed and random factors is 42%.

When missing data values are imputed using missMDA, the contour plots in Fig. 5B show a similar pattern to those of the raw data in Fig. 5A, validating the technique. When LMM analysis is made on the imputed data with 108 observations, it shows that peatland type (*p* < .05), pH (*p* < .001), WT (*p* < .001), and air temperature (*p* < .01) are statistically important factors in determining CH₄ flux. The proportion of variance in CH₄ flux explained by the fixed factor(s) alone is 31%. The proportion of variance explained by both the fixed and random factors is 63% (Table 2).

3.2 | Methane emissions from drained peatlands

A *t*-test shows that the difference in CH₄ emissions between drained (*n* = 61) and natural peatlands (*n* = 42) is significant (*t* = 7.25, *p* < 0.001) (Fig. 6a). Drainage reduced the CH₄ flux by, on average, 84% compared to the original emission values with a mean of 8.3 g C m⁻² year⁻¹. Drainage reduced CH₄ emissions from the fen ecosystems by more than that from bog ecosystems, and a *t*-test showed a significant difference (*t* = 2.46, *p* < .015) between fens and bogs (Fig. 6B). This effect is similar for all types of drained peatland regardless of the land use and vegetation cover. A paired *t*-test to assess the effect of drainage for paired sites of bogs and fens showed that for the bogs (*t* = 4.443; *p* < 0.001; *n* = 25) and for the fens (*t* = 3.762; *p* < 0.01; *n* = 17). A one-way ANOVA shows that the difference in CH₄ emissions after drainage between the land use/land cover of crops (*n* = 4), grass (*n* = 7), natural (*n* = 21), or woodland (*n* = 29) is significant (*F* = 2.98, *p* < 0.05) (Fig. 6c).

3.3 | Methane emissions from restored peatlands

Only 16 sites explicitly measured the effect of rewetting peatlands that had previously been drained for many uses, including forestry, cropping grazing, and mining. There were insufficient data for each category of initial land use, but considering the entire dataset (*n* = 16) rewetting increased methane flux by an average of 1.3 ± 6.5 g C m⁻² year⁻¹ (46%). However, a paired *t*-test showed that the change in CH₄ flux due to rewetting was not statistically significant with mean flux before restoration being 3.0 ± 3.1 g C m⁻² year⁻¹ and after restoration being 4.2 ± 6.3 g C m⁻² year⁻¹ (*p* = .37) with a pooled standard deviation of 6.0 (Fig. 7).

This indicates a different response to rewetting between sites, which all have different previous anthropogenic management, land use, and initial peatland type. The published data are insufficient to identify why CH₄ emissions from the different sites respond differently after rewetting.

TABLE 1 Methane fluxes from natural northern peatlands. MAAT – mean annual air temperature (°C), WT – water table (cm; positive values indicate water depth above the soil surface, and negative values indicate water depth below the soil surface)

Peatland type/ location	Coordinates	D (years)	MAAT (°C)	pH ^a	WT (cm)	Annual CH ₄ flux ^b (g C m ⁻² year ⁻¹)	References
Bog (FIN)	65°51'N, 30°53'E	2	2.0	3.8–4.6	–15 to (–21)	4.0	Alm, Saarnio, Nykänen, Silvola, and Martikainen (1999)
Fen (FIN)				4.1–5.6	–2 to (–40)		
Bog (Dry; Palsa mire; SWE)	68°22'N, 19°03'E	6	–0.7	ND	ND	0.5	Bäckstrand et al. (2010)
Fen (<i>Sphagnum</i> <i>angustifolium</i> ; SWE)					(–5) to (–25)	6.2	
Fen (Wet; <i>Eriophorum</i> spp.; SWE)					–5.0	31.8	
Bog (DE)	53°41'N, 08°49'E	2	8.5	3.1	–10 to (–80)	4.2	Beetz et al. (2013)
Bog (CA)	45°41'N, 75°52'W	2	6.4	ND	–40 to (–50)	2.7	Brown, Humphreys, Moore, Roulet, and Lafleur (2014)
Open bog (CA)	49°10'N, 82°45'W	1	0.0	4–4.8	ND	0.6	Bubier et al. (1993)
Treed bog (CA)				4.6–4.8	ND	0.5	
Open fen/ dry (CA)				5.4–6.3	21.3–81.7	0.0	
Open fen/ wet (CA)				4.8	12.2–12.9	3.8	
Treed fen (CA)				5.4–6.3	2.7–21.3	3.2	
Fen (GL)	74°30'N, 21°00'W	1	–10.3	ND	0 to (–45)	6.7 ^c	Christensen, Friborg, and Sommerkorn (2000)
Bog (USA)	47°32'N, 93°28'W	1	3.0	3.5–7.0	3 to (–43)	9.0	Crill et al. (1988)
Bog (CA)	44°23'N, 65°13'W	2	6.3	ND	11 to (–30)	3.9 ^c	Dalva and Moore (2001)
Bog (SL)	45°59'N, 14°30'W	1	10.0	3.2	–24.4	0.2	Danevcic, Mandic-Mulec, Stres, Stopar, and Hacin (2010)
Bog (USA)	45°94'N, 90°27'W	2	5.7	ND	ND	0.8	Desai et al. (2015)
Bog (hummock; USA)	47°32'N, 93°28'W	2	3.1	ND	–6.1	2.3	Dise, Gorham, and Verry (1993)
Bog (hollow)						9.0	
Junction fen						26.7	
Bog						41.1	
Bog (UK)	55°79'N, 3°24'W	3	10	4.4	–12.5	0.3	Drewer et al. (2010)
Fen (FIN)	67°59'N, 24°12'W	2	–1.4	5.8	1.2	15.0	
Rich fen (CA)	48°21'N, 85°21'W	1	ND	6.3	8.3	154.1 ^c	Godin, McLaughlin, Webster, Packalen, and Basiliko (2012)
Intermediate fen (CA)				6.2	3.0	102.7 ^c	
Poor fen (CA)				4.8	–22.1	1.5 ^c	
Fen (SWE)	64°12'N, 19°34'E	3	1.2	4.0	ND	11.8	Granberg et al. (2001)
Bog (hummock; SWE)	63°44'N, 20°06'E	1	3.3	ND	–19.6	0.9 ^c	Granberg et al. (1997)
Bog (lawn; SWE)					–10.1	2.4 ^c	
Bog (carpet; SWE)					–05.8	1.9 ^c	
Poor fen (SWE)					–15.2	8.4 ^c	
Sedge fen (SWE)	64°20'N, 18°18'E	1		ND	–2.7	4.0 ^c	
Poor fen (SWE)	64°24'N, 20°11'E	1		ND	–3.5	5.3 ^c	

(continues)

TABLE 1 (Continued)

Peatland type/ location	Coordinates	D (years)	MAAT (°C)	pH ^a	WT (cm)	Annual CH ₄ flux ^b (g C m ⁻² year ⁻¹)	References
Poor fen (SWE)	63°44'N, 20°02'E	1		ND	-7.8	2.7 ^c	
Bog (SWE)	63°36'N, 19°37'E	1		ND	-9.5	1.0 ^c	
Poor fen (SWE)	64°02'N, 20°40'E	1		ND	-15.5	0.6 ^c	
Fen (CA)	58°39'N, 93°49'W	4	3.0	ND	-15 to 20	5.1	Hanis, Tenuta, Amiro, and Papakyriakou (2013)
Fen (FIN)	69°14'N, 27°17'E	3	0.4	4.5	0 to (-10)	4.1	Hargreaves, Fowler, Pitcairn, and Aurela (2001)
Fen (treed fen; FIN)	67°00'N, 27°00'E	2	-1.0	ND	-15 to 4	18.1	Huttunen et al. (2003)
Fen (FIN)					-1 to 21	16.3	
Eutrophic fens (FIN)					-26 to 2	11.0	
Fen (spruce mires; FIN)					-37 to (-13)	0.1	
Bog (SWE)	68°20' N, 19°03'E	2	-0.9	ND	ND	20.3	Jackowicz-Korczynski et al. (2010)
Fen (FIN)	60°26' N, 23°38'E	1	ND	4.6–4.7	2.3	18.3 ^c	Juottonen et al. (2012)
	62°16' N, 23°48'E	1	ND	4.9–5.1	-0.9	93.3 ^c	
	64°04' N, 26°40'E	1	ND	5.1–5.3	12.1	30 ^c	
Fen (PL)	52°45' N, 16°18'E	2	6.8	6.2	-4.0	29.2	Juszczak and Augustin (2013)
Bog (CA)	45°41'N, 75°52'W	2	6.0	ND	-19 to (-38.1)	7.9	Lai, Moore, and Roulet (2014)
Blanket bog (IRE)	51°55'N, 9°55'W	3	10.5	4.4–4.7	5 to (-25)	4.7	Laine, Wilson, Kiely, and Byrne (2007)
Open graminoid bog (CA)	61°08'N, 121°04'W	0.2	-3.7	ND	-5 to (-35)	4.9 ^c	Liblik et al. (1997)
Open graminoid fen					-4 to (-9)	3.0 ^c	
Open graminoid poor fen					-8 to (-14)	8.0 ^c	
Open fen (low shrub)					-14 to (-35)	0.9 ^c	
Fen (tree/low shrub)					-39 to (-43)	0.2 ^c	
Bog (tree low/tall shrub)					ND	0.0 ^c	
Fen (CA)	54°95'N, 112°46'W	1	2.1	ND	-30 to (-60)	2.8 ^c	Long, Flanagan, and Cai (2010)
Bog (SWE)	56°15'N, 13°33'E	1	6.2	ND	0 to (-16)	4.3 ^c	Lund et al. (2009)
Bog (SWE)	62°20'N, 18°58'E	1	-0.8	ND	ND	1.5 ^c	
Raised bog (EE)	58°34'N, 24°23'E	1	ND	4.2	ND	1.8	Mander et al. (2012)
Fen (meadow; EE)						1.1	
Bog (hummock; CA)	45°41'N, 75°48'W	5	6.0	ND	-35 to (-52)	4.4 ^c	Moore et al. (2011)
Bog (lawn)					-27 to (-31)		
Bog (<i>Eriophorum vaginatum</i>)					-23 to (-46)		
Fen (hummock; SWE)	MS	1	5.0	ND	-30.0	3.7	Nilsson et al. (2001)
Fen (transitional fens)					-34.0	1.9	
Fen (low sedge fens)					-27.0	6.2	
Fen (tall sedge fens)	64°18'N, 19°33'E				-21.0	12.4	

(continues)

TABLE 1 (Continued)

Peatland type/ location	Coordinates	D (years)	MAAT (°C)	pH ^a	WT (cm)	Annual CH ₄ flux ^b (g C m ⁻² year ⁻¹)	References
Poor fen (SWE)	62°45'N, 31°03'E	2	1.2	4.3 to 5.3	0 to (–20)	11.5	Nilsson et al. (2008)
Fen (FIN)	MS	2	1.9	5.3	–20 to (–117)	26.0	Nykänen, Alm, Lang, Silvola, and Martikainen (1995)
Bog (FIN)	MS	2	2.5	3.7 to 4.3	–1.1 to (–39)	6.9	Nykänen et al. (1998)
Fen	69°49'N, 27°10'E			4.4–5.6		16.4	
Fen (wet; FIN)		2	–1.2	ND	–4.2 to (–4.6)	24.7	Nykänen, Heikkinen, Pirinen, Tiilikainen, and Martikainen (2003)
Bog (dry; FIN)	68°22'N, 19°03'E					1.0	
Bog (SWE)	57°00'N, 82°00'E	2	–0.5	ND	0 to (–35)	1.9	Olefelt et al. (2012)
Bog (RU)	53°54'N, 78°46'W	5	ND	ND	ND	19.4	Panikov and Dedysh (2000)
Rich fen (CA)	53°38'N, 77°43'W	1	–3.1	ND	–8 to (–30)	4.1 ^c	Pelletier, Moore, Roulet, Garneau, and Beaulieu- Audy (2007)
Raised bog	53°34'N, 76°08'W				–6.7 to (–29)	2.9	
Fen (hummock; shrubs)	46°19'N, 86°03'W		–16.6			4.9 ^c	
Poor fen (USA)	61°50'N, 24°12'E	1	5.0	3.8	–5 to (–30)	15 ^c	Pypker et al. (2013)
Boreal fen (FIN)	45°04'N, 78°45'W	2	3.3	ND	–5 to (–50)	9.4	Rinne et al. (2007)
Bog (CA)		1	4.4	4.3–5.5	–29 to (–36)	1.3	Roulet, Ash & Moore (1992)
Fen	50°30'N, 80°23'W			4.8	–114.0	0.3	
Treed fen (shrubs; CA)	64°18'N, 19°33'E 85°13'N, 81°48'W	1	–1.2	ND	ND	0.3	Roulet et al. (1994)
Open fen						0.5	
Open bog						3.5	
Rich bog (shrub)						3.0	
Treed bog						0.1	
Fen (conifer forest)						0.1	
Open fen (CA)	58°45'N, 94°09'W	1	–7.2	ND		5.0	
Treed bog						0.0	
Raised bog (CA)	45°41'N, 75°48'W	6	6.0	3	–20 to (–75)	3.7	Roulet et al. (2007)
Bog (USA)	42°27'N, 84°01'W	3	ND	4.2	–50 to 15	53.7	Shannon and White (1994)
Bog (USA)	58°45'N, 94°09'W		3.9		–50 to 15	18.8	Shannon and White (1994)
Fen (hummock; CA)	46°40'N, 71°10'W	2	ND	ND	–14 to (–21)	1.8	Strack et al. (2004)
Fen (lawn; CA)		2	ND	ND	–6 to (–14)	2.8	
Fen (hollow; CA)		2	ND	ND	0 to (–20)	2.2	
Treed bog (CA)	47°96'N, 69°42'W	1	5.2	ND	–15.3	6.6	Strack & Zuback (2013)
Boreal fen (USA)	53°57'N, 105°57'W	1	ND	7.1	–5 to (30)	17.7 ^c	Suyker, Verma, Clement, and Billesbach (1996)
Fen (SWE)	ND	2	–0.7	ND	ND	20.2	Tang et al. (2015)
						22.6 ^M	
Poor fen (USA)	43°12.5'N, 71°3.5'W	5	8.1	4.1–5.7	9.4 to 29.9	31.0 ^c	Treat et al. (2007)
Fen (CA)	54°06'N, 72°30'W	2	–4.3	ND	–5.4 to (–16.3)	6.3	Trudeau, Garneau, and Pelletier (2013)
Rich fen (USA)	64°82'N, 147°87'W	2	–2.9	5.3	ND	2.8 ^c	Turetsky et al. (2008)

(continues)

TABLE 1 (Continued)

Peatland type/ location	Coordinates	D (years)	MAAT (°C)	pH ^a	WT (cm)	Annual CH ₄ flux ^b (g C m ⁻² year ⁻¹)	References
Fen (CZ)	49°09'N, 13°22'E	3	4.0	ND	-7.2 to (-45.2)	51.8 ^c	Urbanova, Barta, and Pícek (2013)
Bog (CZ)	48°58'N, 13°27'E	3	3.2	ND	-2.9 to (-36.1)	10.4 ^c	
Bog (low shrub; CZ)	48°58'N, 13°27'E	2	3.2	ND	-2.3 to (-10.6)	8.9 ^c	Urbanova, Pícek, and Tuittila (2013)
Bog (<i>Trichophorum</i> lawn)				ND		10.1 ^c	
Eccentric bog (SWE)	63°44'N, 20°06'E	2	ND	ND	-30 to 124	4.0	Waddington and Roulet (2000)
Fen (RU)	72°22'N, 126°30'E	1	-14.7	ND	-10.0	2.4	Wille, Kutzbach, Sachs, Wagner, and Pfeiffer (2008)
Bog (UK)	MS	1	5.8	6.0	-20.0	7.1	Worrall, Reed, Warburton, and Burt (2003)
Bog (UK)	54°09'N, 04°11'W	2	9.4	3.6	-15.3	5.8	Yamulki et al. (2013)

D, duration (years); ND, no data; M, modeled; MS, multiple sites; CA, Canada; CZ, Czech Republic; EE, Estonia; FIN, Finland; DE, Germany; GL, Greenland; IRE, Ireland; PL, Poland; RU, Russia; SL, Slovenia; SWE, Sweden; UK, United Kingdom; and USA, United States of America.

^aDifferent methods were used to measure soil pH using pH probe/meter in deionized water or 0.01 M CaCl₂ in 1:1 and 1:2, or 1:5 (v:v) soils: solution ratios.

^bAverage values were measured/calculated and converted to g C m⁻² year⁻¹ using original data.

^cAnnual values were estimated from the original seasonal measured values. Methane gas flux during winter was considered as 15% from the annual flux following the suggestions of Saarnio et al. (2007) and Maljanen et al. (2010).

4 | DISCUSSION

4.1 | Methane emissions from northern natural peatlands

This review and meta-analysis shows that natural northern peatlands are a significant source for CH₄ emissions to the atmosphere due to prevailing waterlogged conditions (Huttunen, Nykänen, Turunen, & Martikainen, 2003). This is in agreement with other previous studies carried out by Nilsson et al. (2001), Christensen et al. (2003), Zhuang et al. (2006), Lai (2009) and Turetsky et al. (2014). However, high variability was observed between the sites with 95% CI of 7.6–15.7 g C m⁻² year⁻¹ for the mean and 3.3–6.3 g C m⁻² year⁻¹ for the median, especially on flooded peatlands (Couwenberg & Fritz, 2012). The type and composition of dominant peatland vegetation (Bubier, 1995; Turetsky et al., 2014) influence CH₄ emission dynamics, both by adding labile C substrates for CH₄ production (Ström, Ekberg, Mastepanov, & Christensen, 2003) and by maintaining gas conduits, which affect the production, oxidation, and transportation of CH₄ (Joabsson et al., 1999). Bogs and fens differ in biotic and abiotic factors. These biotic and abiotic differences lead to the fens having the highest methanogenic activity (Juottonen et al., 2005), highest litter degradation rate (Aerts, Verhoeven, & Whigham, 1999), and thereby highest CH₄ emissions (Nykänen et al., 1998), compared to the bogs. However, both fen and bog ecosystems (Granberg et al., 1997; Lund, Christensen, Mastepanov, Lindroth, & Strom, 2009; Nilson et al., 2001; Rinne et al., 2007) are sources for CH₄ emissions which may cause these peatland types to be a net GHG source to the atmosphere (Drewer et al., 2010). The microtopography of a peatland is not uniform, with many

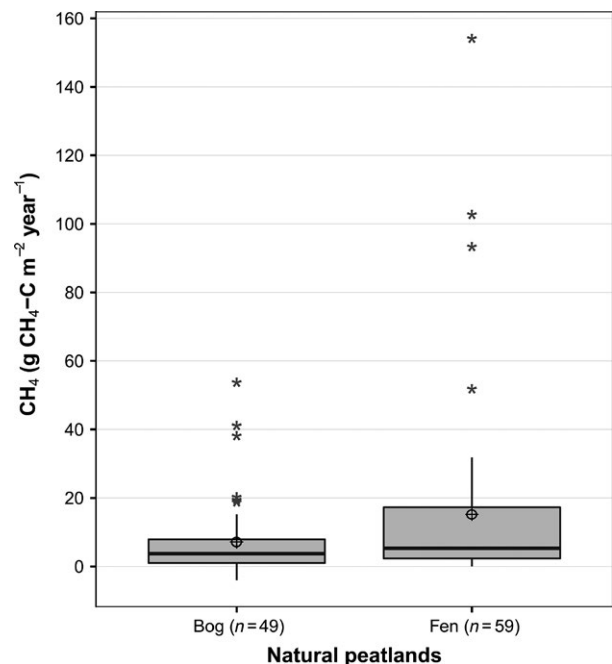


FIGURE 2 Box and whiskers plot showing median, 25 and 75% median quartiles, mean (⊕), 95% confidence interval (whiskers), and outlier (*) values of mean annual methane emissions per peatland type. T-test indicates a significant difference ($t = -1.99$; $p < .05$) between the two groups

hummocks and hollows, which can result in highly variable CH₄ emissions from the same site (Lai, 2009). Differences in methane emissions between the hummocks and hollows could be explained by the higher CH₄ oxidation in the thicker aerobic acrotelm layers of the hummocks

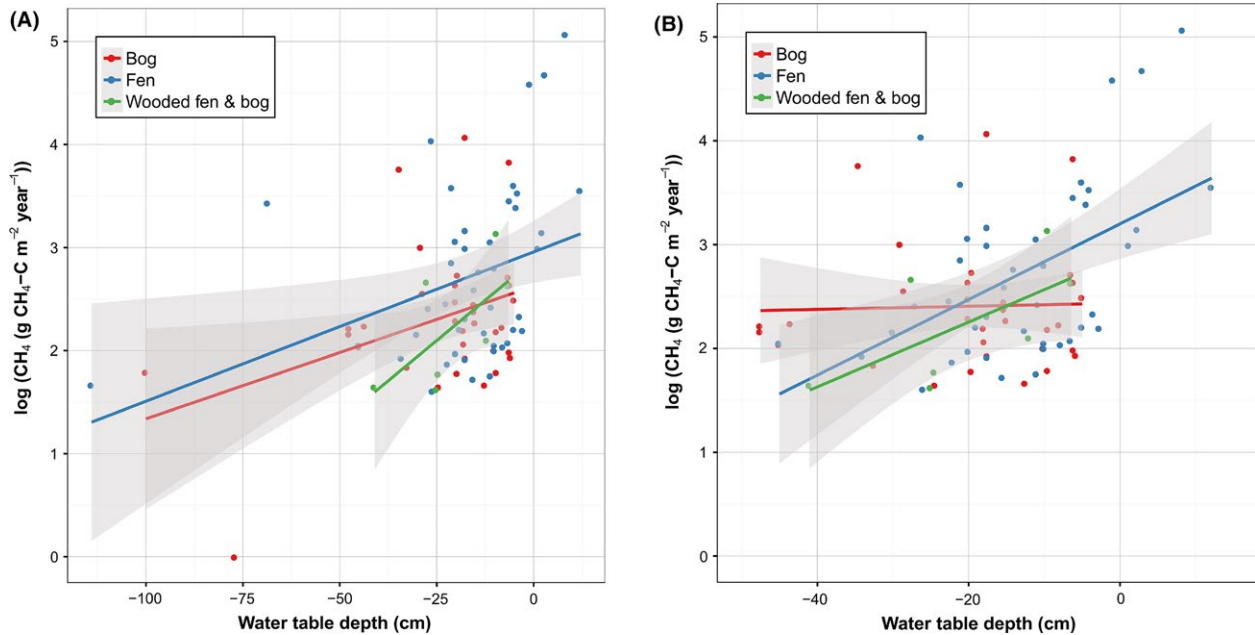


FIGURE 3 Relationships between annual CH_4 flux and mean annual water table in different peatland types: (A) using all available data: bog ($n = 35$, $r^2 = .11$, $p < .05$), fen ($n = 45$, $r^2 = .13$, $p < .01$), and wooded fen and bog ($n = 7$, $r^2 = .36$, $p = .09$); (B) when 4 outliers are removed: bog ($n = 33$, $r^2 = .36$, $p = .8$), fen ($n = 43$, $r^2 = .22$, $p < .001$), and wooded fen and bog ($n = 7$, $r^2 = .36$, $p = .09$). The shaded area represents 95% confidence intervals of the linear regression trend lines

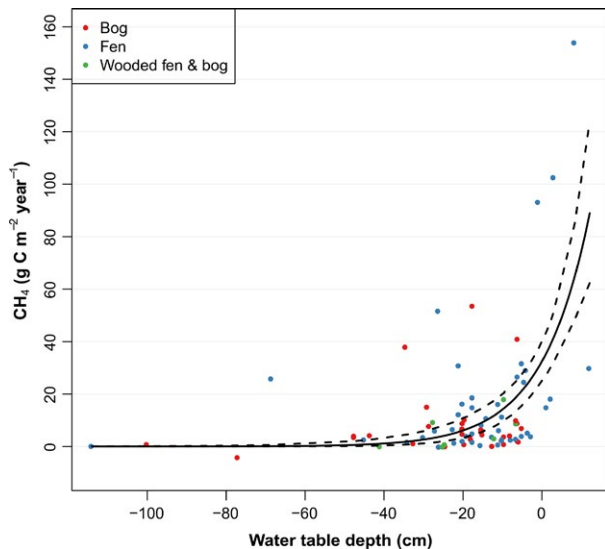


FIGURE 4 Exponential fitted regression of annual CH_4 flux and mean annual water level. Methane flux: $\text{CH}_4 = 32.462 \times \exp^{(0.08 \times \text{WT})}$ ($n = 87$, $r^2 = .54$, $p < .01$). The dashed lines represent 95% confidence intervals for the regression line

(Waddington and Roulet, 1996) and the higher CH_4 productions in the hollows due to high WT and temperature (Bubier et al., 1993).

A number of dynamic biological processes control CH_4 emissions from northern peatlands. However, gas production and consumption are mainly due to methanogenic and methanotrophic microbiota, respectively. Methane transport to the atmosphere takes place either physically (by diffusion and ebullition) or biologically (by a plant-mediated process) (Lai, 2009). Our analysis suggests that the emission

of CH_4 from northern peatlands is mainly controlled by WT depth (Granberg et al., 1997; Moore & Knowles, 1989), plant community composition (Granberg et al., 1997; Nilsson et al., 2001), and soil pH (Hutsch, 1998; Singh et al., 1999). Nevertheless, the influence of soil pH on CH_4 emissions is uncertain because laboratory-measured soil pH may differ from field pH. Our analysis shows that the optimal WT for CH_4 emissions was consistently below the peat surface in the bogs and near to the peat surface for the fens. A similar conclusion was also reported by Turetsky et al. (2014). Many studies have reported the influence of WT depth (Frenzel & Karofeld, 2000; Granberg et al., 1997; Moore & Dalva, 2006; Yang et al., 2006), pH (Hutsch, 1998; Singh et al., 1999), and temperature (Ding & Cai, 2007; Granberg et al., 1997; Saarnio et al., 1998) on CH_4 emissions. Deep WT can reduce CH_4 emissions from peatlands (Strack, Waddington, & Tuittila, 2004), but it may encourage the domination of vascular plant species over mosses which can increase CH_4 production (Bellisario, Bubier, & Moore, 1999). In this review, however, mean annual air temperature is not a strong predictor for CH_4 emissions, and the interaction between mean annual air temperature, plant community composition, and soil WT depth is important (Granberg et al., 1997) [e.g., a clear relationship of CH_4 emissions on soil temperature at certain WT depth reported by Nadeau, Rousseau, Coursole, Margolis, and Parlange (2013) and Olson, Griffis, Noormets, Kolka, and Chen (2013)]. Here, we observe that CH_4 emissions are highest at a MAAT around 2°C , decreasing above and below that value.

The response of CH_4 emissions in peatlands to temperature appears to be somewhat unpredictable. Most of the studies report a clear dependence of CH_4 emission intensity on the soil temperature (Christensen et al., 2003; Gedney, Cox, & Huntingford, 2004;

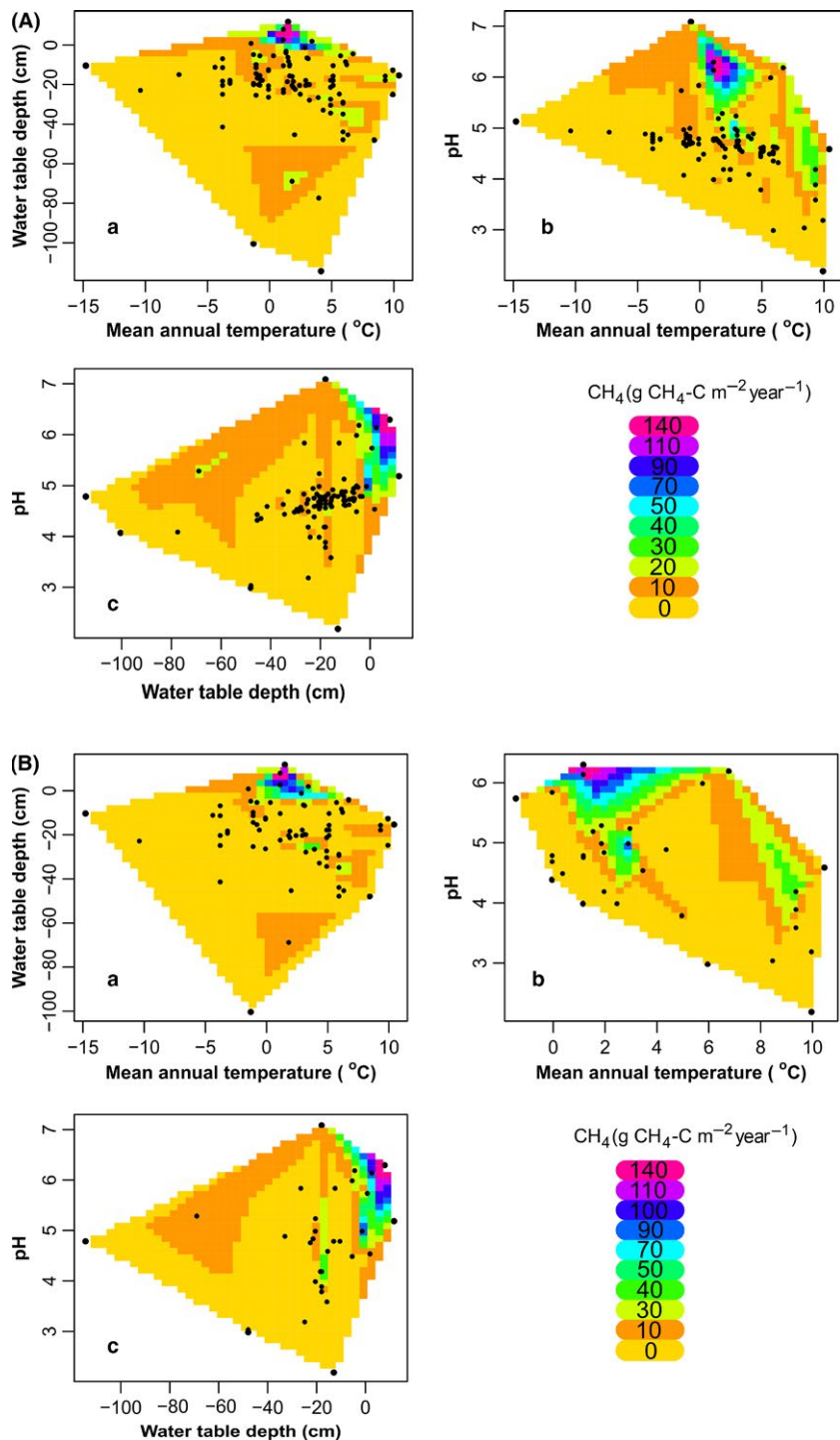


FIGURE 5 Contour plots of imputed data showing relationships between the annual CH_4 flux and environmental parameters: (A) when only available data used: (a) mean annual temperature and mean water table below the surface ($n = 76$). These two variables explain 8.5% of CH_4 flux overall variation ($p < .05$); (b) mean annual temperature and soil pH ($n = 33$). These two variables explain 16.3% of CH_4 flux overall variation ($p < .05$); (c) soil pH and mean water table below the surface ($n = 32$). These two variables explain 17.8% of CH_4 flux overall variation ($p < .05$). (B) when data were imputed ($n = 108$): (a) mean annual temperature and mean water table below the surface. These two variables explain 7.6% of CH_4 flux overall variation ($p < .01$); (b) mean annual temperature and soil pH. These two variables explain 19.7% of CH_4 flux overall variation ($p < .001$); (c) soil pH and mean water table below the surface. These two variables explain 16.0% of CH_4 flux overall variation ($p < .05$)

Mastepanov et al., 2013; Treat et al., 2007; Updegraff, Bridgman, Pastor, Weishampel, & Harth, 2001). Likewise, models of CH_4 emission consider soil temperature as a main driver (Bridgman, Cadiello-Quiroz, Keller, & Zhuang, 2013; Walter & Heimann, 2000). However, a combined chamber and eddy covariance study by Pypker, Moore, Waddington, Hribljan, and Chimner (2013) shows that daily mean soil temperature at 20 cm depth was poorly correlated with changes in CH_4 (17%) when the ecosystem represented a net CO_2 sink (negative net ecosystem exchange, NEE), but the correlation increased to 34% when it was a net CO_2 source (positive NEE). This indicates shifting

temperature controls on the CH_4 flux throughout the growing season (Treat et al., 2007).

Natural northern peatlands have an important impact on climate change (Christensen et al., 2003; Lai, 2009; Nilsson et al., 2001; Turetsky et al., 2014), and climate change has an impact on northern peatlands. In the Nordic region, under climate change, temperature is predicted to increase and WT to decrease (Forster et al., 2007). Temperature may accelerate changes in soil microbial processes, vegetation dynamics, and chemistry of pore water, all of which will affect CH_4 cycling (Weltzin, Bridgman, Pastor, Chen, & Harth, 2003; White,

FIGURE 6 Effects of drainage on CH_4 emissions from peatlands. Box and whiskers plots showing median, 25 and 75% median quartiles, mean (\oplus), 95% confidence interval (whiskers), and outlier values (*). (A) Comparison of annual CH_4 flux from drained and natural peatlands. T-test indicates a significant difference ($t = 7.25$; $p < .001$) between the two groups, (B) CH_4 flux of drained peatland by type, bog and fen, and t-test indicates a significant difference between bog and fen ($t = 2.46$; $p < .05$). (C) CH_4 flux of drained peatland by land use: cropland, grassland, natural, and woodland/shrubs; ANOVA shows significant differences between the four groups ($F = 2.98$; $p < .05$)

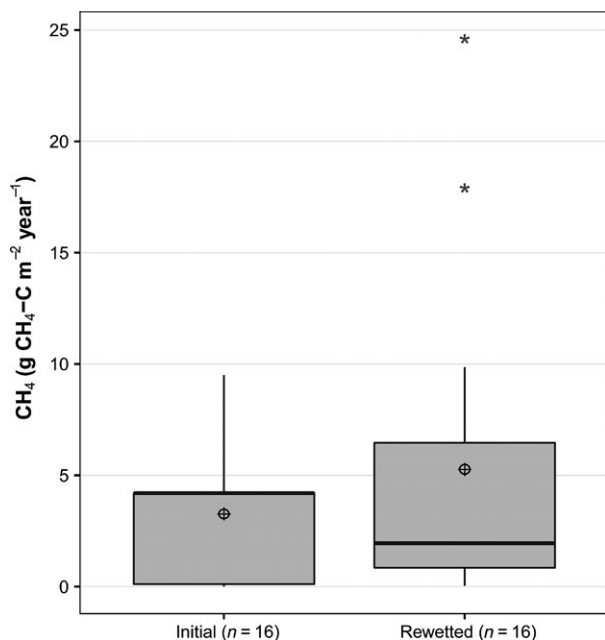
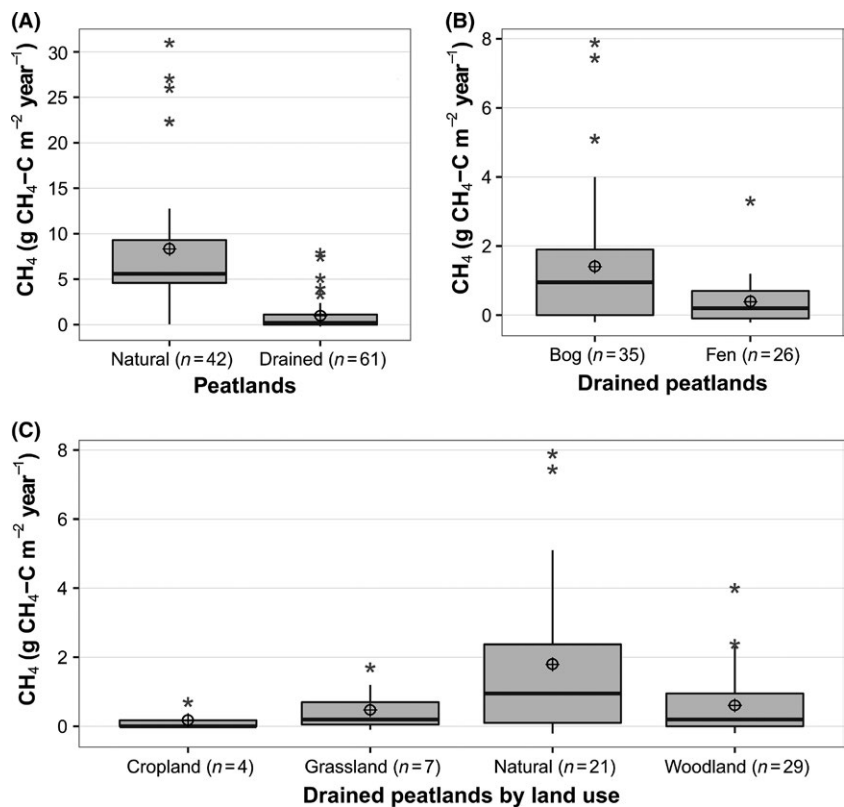


FIGURE 7 Effects of rewetting on annual CH_4 flux from peatlands. Box and whiskers plots showing median, 25 and 75% median quartiles, mean (\oplus), 95% confidence interval (whiskers), and outlier values (*). The left box shows initial methane flux with anthropogenic drained land management, whereas the right one indicates CH_4 flux after restoring vegetation and/or rewetting

Shannon, Weltzin, Pastor, & Bridgman, 2008). High temperature will also result in melting of the permafrost and release of CH_4 to the atmosphere, which may provide a positive feedback to climate change

in the short term (Friedlingstein et al., 2006; Olefeldt, Turetsky, Crill, & McGuire, 2013). The larger unsaturated zone will lead to less CH_4 emissions, and some dry sites may become sinks for CH_4 (Worrall, Burt, & Adamson, 2006). McCalley et al. (2014) reported that microbial community response to permafrost thaw will regulate CH_4 dynamics. However, the majority of models forecast a significant warming-related decrease of CH_4 emissions from northern peatlands (Bridgman et al., 2013; Froking et al., 2011). In most temperate wetlands, over the long term (300 years), C sequestration is expected to compensate for the warming role of CH_4 , turning most wetlands to net C sinks with net negative radiative forcing (Mitsch et al., 2013).

4.2 | Methane emissions from drained peatlands

The drainage practices in northern peatlands clearly reduce CH_4 emissions under all types of land use and vegetation, on average by 84% (Table 3). Drainage practices improve aeration (Schrier-Uijl, Veenendaal, Leffelaar, van Huissteden, & Berendse, 2010) leading to lower CH_4 emissions. They decrease C input, from decomposing plants, to the methanogenic anaerobic layer (Basiliko, Yavitt, Dees, & Merkel, 2003; Bergman, Svensson, & Nilsson, 1998; Bergman et al., 2000). Drainage also increases CH_4 oxidation to CO_2 and thereby reduces CH_4 emissions (Holden, 2005; Moore & Dalva, 2006; Sundh, Nilsson, Mikkela, Granberg, & Svensson, 2000). Moreover, Yrjälä et al. (2011) found that several years of drying changed the structure of the plant community and thereby microbial communities that control functions of GHG emissions. Similar results of decrease in CH_4 emissions under drainage were reported by Bussell, Jones, Healey, and

	Estimates	SE	df	T value	p-value ^{††}
Intercept	0.387	0.562	100	0.602	.55
Peatland type	0.271	0.122	91	2.224	.03*
pH	0.465	0.112	102	4.134	7.32e ^{-5***}
Water table	0.125	0.004	103	3.549	.58e ^{-3***}
Air temperature	0.514	0.019	80	2.687	.88e ^{-2**}

Missing values were imputed using missMDA software. This produced 108 observations for LMM analysis. Peatland type, pH, WT, and air temperature are statistically important factors in this case. The proportion of variance explained by the fixed factor(s) alone is 31% of CH₄ flux variation. The proportion of variance explained by both the fixed and random factors is 63%.

^{††}Significant codes: 0 = ***; 0.001 = **; 0.01 = *.

TABLE 2 Relationships between annual CH₄ flux and environmental variables (WT and pH) and type of peatland using linear mixed-effects model (LMM)

Pullin (2012) and Turetsky et al. (2014). However, drainage influences CH₄ emissions from fens more than from bogs. This is because WT depth in the fen sites is more sensitive to drainage compared to the bog sites (Maljanen et al., 2010).

Drainage ditches themselves can become new anaerobic zones, with similar characteristics to the undrained peat, with similar or even increased CH₄ emissions (Huttunen et al., 2003; Schrier-Uijl et al., 2010; Sundh et al., 2000). In fen meadows in the Netherlands, Schrier-Uijl et al. (2010) found that ditches and bordering edges contributed up to 60–70% of the total farms' CH₄ emissions. These higher emissions from drainage ditches could be large enough to compensate for the reduced CH₄ emissions by drainage on the remainder of the drained peatland area (Minkinen, Byrne, & Trettin, 2008). In contrast, Minkinen, Laine, Nykänen, and Martikainen (1997) reported that CH₄ emissions from ditches in a drained peatland plantation in Finland during the summer represent about only 4.5% of CH₄ emissions. Sundh et al. (2000) found that CH₄ emissions from harvested and drained peat can be kept lower than that from virgin peatland by keeping the ditches clear and free from vegetation.

Drainage and cultivation result in significant reductions in CH₄ emissions, although it may increase other GHG emissions, that is, CO₂ and N₂O (Oleszczuk, Regina, Szajdak, Höper, & Maryga-nova, 2008). The microbial production of CH₄ is anaerobic, while the production of CO₂ is aerobic. Therefore, the production and consumption of these two greenhouse gases in peat soils are highly dependent on the oxygen availability in the soil and, thus, the depth of the water table (Aerts & Ludwig, 1997). In fen and bog peatlands, drainage decreased CH₄ emission but increased CO₂ emission by more than one order of magnitude (Von Arnold, Nilsson et al., 2005; Von Arnold, Weslien et al., 2005; Yamulki, Anderson, Peace, and Morison (2013). This reduction in CH₄ emissions, in association with the primary productivity of vegetation, could decrease the total climate forcing of peatlands over the coming century (Worrall et al., 2011). There is a probability of 69% that drainage will result in an overall improvement in the GHG budget due to less CH₄ emissions (Worrall et al., 2011). Nevertheless, the timescale over which this GHG budget is calculated has an influence, since loss of CO₂ after drainage can be very long-lasting (Maljanen et al., 2010). In contrast, Oleszczuk et al. (2008) noted that drainage could increase CO₂ emissions, with CO₂ having a longer atmospheric lifetime relative to CH₄, so the loss of C and lower C sink capacity in

drained peatlands could result in increased climate forcing over time. This uncertainty in CH₄ changes over time is due to the limited long-term (>10 years) studies on drained northern peatlands.

4.3 | Methane emissions from restored peatlands

Restoration of drained northern peatlands by rewetting increased CH₄ emissions compared to the original prewetting emission. In this meta-analysis, restoration increased CH₄ flux by 46% (Table 4). Here, the open water pools behind ditch blocks increase the gas emissions (Baird, Holden, & Chapman, 2009). Hahn-Schoffl et al. (2011) reported significantly higher CH₄ emissions from flooded fen grasslands in Germany, because of high availability of fresh organic matter. Methane emission could be reduced by creating different vegetation compositions (Komulainen, Nykänen, Martikainen, & Laine, 1998; Tuittila et al., 2000; Waddington & Day, 2007) that lead to changes in the methanogenic community and peat properties (Basiliko, Knowles, & Moore, 2004). Mahmood and Strack (2011) reported a significant correlation between CH₄ emissions and vegetation cover on an abandoned peatland. This is because vegetation stimulates CH₄ emissions by providing substrates for gas production and transportation to the atmosphere (Wilson, Farrell, Muller, Hepp, & Renou-Wilson, 2013). In Canada and Ireland, CH₄ emissions from restored cutover peatlands increased in the first 3 years following restoration due to the fresh substrates provided by the new vegetation cover (Waddington & Day, 2007; Wilson et al., 2013). Fast decomposing litter following restoration of a bog peat could result in higher CH₄ flux, which could dominate GHG emissions up to 30 years following rewetting (Vanselow-Algan et al., 2015).

As discussed earlier, vascular plants can play an important role in transporting CH₄ from soils to the atmosphere through aerenchyma (Couwenberg & Fritz, 2012; Henneberg, Elsgaard, Sorrell, Brix, & Petersen, 2015). The establishment of vascular vegetation following extraction is generally more extensive on cutover fens than on cutover bogs (Graf, Rochefort, & Poulin, 2008). Although a combined transportation of O₂ with CH₄ by aerenchyma tissues could reduce CH₄ emissions, previous studies reported higher emissions from vascular plants, especially sedges (Waddington, Roulet, & Swanson, 1996). Roulet, Ash, and Quinton (1993) and Roulet and Moore (1995) reported approximately 23–57 times greater CH₄ emissions from

TABLE 3 Methane fluxes from drained peatlands

Peatland type/ location	Coordinates	D (years)	Trophic level/ vegetation	CH ₄ flux ^a (g C m ⁻² year ⁻¹)			References
				Natural	Drained	% change	
Bog (FIN)	MS	2	Ombrotrophic	4.0	2.1	-48	Alm et al. (1999)
Fen (FIN)	MS	2	Oligotrophic	31.0	0.0	-100	
Fen (DE)	52°30'N, 08°20'E	4	Cropland	ND	0.7		Beyer, Liebersbach, and Höper (2015)
Fen (DE)			Grassland	ND	-0.1		
Bog (EE)	58°52'N, 26°14'E	2	Ombrotrophic	2.7	0.9	-66	Carter, Sutton, and Stenglen (2012)
Blanket bog (UK)	52°58'N, 03°49'W	2.3	<i>Eriophorum vaginatum</i> ; <i>Sphagnum</i> spp.	4.5	3.3	-27	Cooper et al. (2014)
Bog (forest; SL)	45°58'N, 14°28'E	1	<i>Betula</i> spp., <i>Frangula alnus</i>	0.2	-0.2	>-100	Danevcic et al. (2010)
Fen (SL)	45°58'N, 14°28'E	1	Grassland; WT = -53.2 cm	ND	0.2	n/a	
Fen (SL)		1	Grassland; WT = -96.7 cm	ND	0.2	n/a	
Bog (UK)	55°47'N, 3°14'W	2	Patchy mix of grasses, sedges & soft rush	ND	0.1	n/a	Dinsmore, Skiba, Billett, and Rees (2009)
Bog (cropland; CA)	45°08'N, 73°26'E	1	Onion	ND	0.0	n/a	Glenn, Heyes, and Moore (1993)
			Celery		0.0	n/a	
			Occasional shrubs/ herb		0.0	n/a	
Bog (forest; CA)			Trees/ shrub/ herb		0.0	n/a	
			Trees/ shrub/ herb		0.0	n/a	
Bog (cropland; CA)	45°09'N, 73°40'E	1	Celery	ND	0.0	n/a	Glenn et al. (1993)
			Grass		0.0	n/a	
Bog (forest; CA)			Trees/ shrub/ herb		0.0	n/a	
Bog (FIN)	60°38'N, 24°21'E	1.3	Dwarf shrub pine	ND	-0.1	n/a	Lohila et al. (2011)
Fen (cropland; FIN)	MS	5	Birch-pine-alder	ND	-0.1	n/a	Mäkiranta et al. (2007)
Fen (cutaway peat)			Birch-pine		0.0	n/a	
Bog (afforested; FIN)	64°06'N, 24°21'E	2	Birch; 1 year old	ND	1.0 ^b	n/a	Maljanen, Hytönen, and Martikainen (2001)
Bog (afforested)			Pine; 6 years old		0.7 ^b	n/a	
Bog (afforested)			Pine; 23 years old		-0.1 ^b	n/a	
Fen (FIN)	MS	2	<i>Eriophorum angustifolium</i>	5.6	0.2	-96	Minkinen and Laine (2006)
			<i>E. vaginatum</i>		-0.1	>-100	
			<i>Sphagnum</i> sp.		-0.1	>-100	
			Forest moss		-0.2	>-100	
			Litter		-0.1	>-100	
Bog (FIN)	MS	2	<i>E. vaginatum</i>	5.0	5.1	2	
			<i>Sphagnum angustifolium</i>		1.4	-71	
			Forest moss		0.4	-93	
Fen (forest; FIN)		3	Mesotrophic treed	0.1	0.0	-100	Minkinen, Korhonen, Savolainen, and Laine (2002)
			Mesotrophic treeless	0.1	0.0	-100	
			Mesotrophic sparsely treed	9.0	1.1	-88	

(continues)

TABLE 3 (Continued)

Peatland type/ location	Coordinates	D (years)	Trophic level/ vegetation	CH ₄ flux ^a (g C m ⁻² year ⁻¹)			References
				Natural	Drained	% change	
Raised bog (FIN)			Oligotrophic treed	22.3	1.0	-96	
			Oligotrophic treeless	4.9	1.1	-77	
			Oligotrophic sparsely treed	22.3	1.0	-96	
			Ombrotrophic treed	22.3	1.0	-96	
			Ombrotrophic treed	5.4	1.2	-77	
			Ombrotrophic treeless	11.7	7.4	-36	
			Ombrotrophic sparsely treed	4.9	2.3	-53	
Blanket bog (forest; UK)	55°10'N, 02°03'W	2	Sitka spruce	1.3	0.5	-65	Mojeremane, Rees, and Mencuccini (2010)
Fen (FIN)	62°45'N, 31°03'E & 62°40'N, 30°50'E	2	Virgin fen	26.0	0.1	-100	Nykänen et al. (1995)
Bog (FIN)	62°45'N, 31°03'E & 62°40'N, 30°50'E	2	Ombrogenous bog	13.0	7.9	-38	Nykänen (1998)
			Ombrogenous pine forest	5.3	2.4	-55	
			Dwarf shrub pine bush	5.9	1.1	-81	
			Minerogenous oligotrophic	27.1	-0.2	>-100	
			Minerogenous mesotrophic	1.0	0.9	-4.4	
Bog (EE)	MS	1	Ombrotrophic	8.5	2.4	-72	Salm et al. (2012)
Fen (CA)	46°40'N, 71°10'W	2	Hummocks	1.8	0.2	-89	Strack et al. (2004)
			Lawns	2.8	1.2	-57	
			Hollows	2.2	3.3	50	
Fen (USA)	64°82'N, 147°87'W	2	Rich fen/ Warm	2.8 ^b	1.8 ^b	-36	Turetsky et al. (2008)
			Rich fen/ unwarm	2.2 ^b	1.3 ^b	-41	
Bog (CZ)	49°10'N, 13°19'E	2	High shrubs	10.8	0.2 ^b	-98	Urbanova, Barta et al. (2013)
			<i>Molinia caerulea</i>	9.4	1.7 ^b	-82	
			<i>M. caerulea</i> ; <i>Calluna vulgaris</i> ; <i>E. vaginatum</i> & <i>Vaccinium uliginosum</i>	9.4	4.0 ^b	-57	
Fen (forest; SWE)	57°8'N, 14°45'E	2	Black alder	5.7	0.7	-88	Von Arnold, Nilsson et al. (2005)
			Downy birch		0.7	-88	
Fen (forest; SWE)	57°8'N, 14°45'E	2.5	Norway spruce (young trees)	8.6	0.0	-100	Von Arnold, Weslien et al. (2005)
			Norway spruce (old trees)		0.2	-98	
			Pine		0.8	-91	

D, duration (years); ND, no data; MS, multiple sites; WT, water table (cm; positive values indicate water depth above the soil surface, and negative values indicate water depth below the soil surface). n/a, not applicable; CA, Canada; CZ, Czech Republic; EE, Estonia; FIN, Finland; DE, Germany; SL, Slovenia; SWE, Sweden; and UK, United Kingdom.

^aAverage values were measured/calculated and converted to g C m⁻² year⁻¹ using original data. A negative value indicates CH₄ uptake, and a positive value indicates CH₄ emission.

^bAnnual values were estimated from the original seasonal measured values. Methane flux during winter was considered as 15% from the annual flux following the suggestions of Saarnio et al. (2007) and Maljanen et al. (2010).

TABLE 4 Effects of restoration on CH₄ fluxes from peatlands

Peatland type/location	Coordinates	D (years)	Type of management/vegetation	CH ₄ flux ^a (g C m ⁻² year ⁻¹)			References
				Natural	Restored	% change	
Bog (DE)	53°41'N, 8°49'E	2	Rewetted (intensive grassland)	4.2	0.1	-97	Beetz et al. (2013)
		2	Rewetted (extensive grassland)	4.2	0.9	-79	
Bog (DE)	53°00'N, 07°32'E	2	Dry/ <i>Sphagnum cuspidatum</i> / <i>Eriophorum angustifolium</i>	4.2 ^b	0.0	-100	Beyer and Höper (2015)
			<i>Wet/S. cuspidatum</i> / <i>E. angustifolium</i>	4.2	1.7	-60	
			Deep peat, wet/ <i>S. cuspidatum</i> / <i>E. angustifolium</i>	4.2	0.7	-83	
			Peat extraction/peat mosses cultivation/ <i>Sphagnum</i> <i>papillosum</i> / <i>E. angustifolium</i>	4.2	0.6	-86	
Blanket bog (UK)	52°58'N, 03°49'W	2.3	Rewetted/ <i>Eriophorum vaginatum</i>	4.5	9.0	100	Cooper et al. (2014)
Fen (NL)	52°11'N, 5°43'E	2	Grasses, reeds and forbs	ND	31.8	n/a	Hendriks, van Huissteden, Dolman, and van der Molen (2007)
Fen (forest; FIN)	MS	1	Restored/forestry	ND	0.9 ^c	n/a	Juottonen et al. (2012)
Fen (FIN)	61°48'N, 24°17'E	3	Rewetted/cotton grass	0.1	1.6	>100	Komulainen et al. (1998)
Bog (FIN)	61°51'N, 24°14'E	3	Rewetted/cotton grass	0.6	3.5	>100	
Blanket bog (UK)		0.1	<i>E. vaginatum</i>	ND	6.9 ^c	n/a	McNamara, Plant, Oakley, and Ostle (2008)
			<i>S. angustifolium</i>		2.7 ^c	n/a	
			Mixed grasses		0.0 ^c	n/a	
			<i>C. vulgaris</i>		0.0 ^c	n/a	
Treed bog (CA)	47°06'N, 69°42'W	1	Restored field/sedge	6.6	0.4	-95	Strack and Zuback (2013)
			Restored ditch/sedge		15.5	>100	
			Restored site/sedge		1.4	-79	
Bog (CZ)	48°58'N, 13°27'E	2	Rewetted <i>Trichophorum</i> spp. lawn	9.5	5.9 ^c	-88	Urbanova, Pícek et al. (2013)
Bog (CZ)		2	Rewetted high shrub	9.5	1.2 ^c	-38	
Bog (DE)	53°44'N, 09°50'E		Rewetted heath	ND	47.8 ^c	n/a	Vanselow-Algan et al. (2015)
Bog (DE)	53°44'N, 09°50'E	1	Rewetted <i>Sphagnum</i> spp.		74.7 ^c	n/a	
			Rewetted purple moor grass		111.4 ^c	n/a	
			Rewetted industrial extraction		0.2 ^c	n/a	
Bog (CA)	47°58'N, 69°25'W	4	Restored/peat	0.0 ^c	0.0 ^c	0	Waddington and Day (2007)
			Restored/moss	5.5 ^c	0.0 ^c	>-100	
			Restored/shrub	-0.2 ^c	0.1 ^c	67	
			Restored/herbaceous	-0.1 ^c	2.2 ^c	>100	

(continues)

TABLE 4 (Continued)

Peatland type/location	Coordinates	D (years)	Type of management/vegetation	CH ₄ flux ^a (g C m ⁻² year ⁻¹)			References
				Natural	Restored	% change	
			Restored/ditch	0.1 ^c	24.6 ^c	>100	
			Cutover/peat	0.0 ^c	-0.1 ^c	-67	
			Cutover/moss	1.5 ^c	0.1 ^c	>-100	
			Cutover/shrub	0.1	0.1 ^c	0	
			Cutover/herbaceous	-0.2 ^c	-0.1 ^c	100	
			Cutover/ditch	-0.1 ^c	17.9 ^c	>100	
Blanket bog (IRE)	54°07'N, 09°35'W	3	Rewetted/ <i>Juncus</i> spp., <i>Sphagnum</i> spp.	0.1 ^c	8.2	>100	Wilson et al. (2013)
			Rewetted/ <i>Sphagnum</i> spp.		9.9	>100	
			Rewetted/ <i>Eriophorum</i> spp.		5.3	>100	
Treeless bog (DE)	62°12'N, 23°18'E	1	Restored/ <i>Sphagnum riparium</i>	ND	14.1	n/a	Yli-Petäys, Laine, Vasander, and Tuittila (2007)

D, duration (years); n/a, not applicable; ND, no data; CA, Canada; CZ, Czech Republic; FIN, Finland; DE, Germany; IRE, Ireland; NL, the Netherlands; UK, United Kingdom; and USA, United States of America.

^aAverage values were measured/ calculated and converted to g C m⁻² year⁻¹ using original data. A negative CH₄ value indicates uptake, and a positive CH₄ value indicates emission.

^bValue from Beetz et al. (2013).

^cAnnual values were estimated from the original seasonal measured values. Methane gas flux during winter was considered as 15% from the annual flux (Maljanen et al., 2010; Saarnio et al., 2007).

restored herbaceous vegetation than from a herbaceous vegetation cutover site. Moreover, common cotton grass (*Eriophorum vaginatum*) generates large CH₄ fluxes (Greenup, Bradford, McNamara, Ineson, & Lee, 2000), whereas peat mosses (*Sphagnum* spp) can act as a CH₄ sink (Raghoebarsing et al., 2005) following restoration.

Changes with time in CH₄ patterns after rewetting may be related to previous land use. However, although restoration increases CH₄ fluxes, it could generally reduce net GHG emissions by reducing CO₂ flux (Baird, Belyea, & Morris, 2009; Beetz et al., 2013; Samaritani et al., 2011; Strack & Zuback, 2013). Published data on CH₄ emissions from long-term (>10 years) rewetted northern peatlands are limited and therefore, changes in gas emissions over time remain uncertain.

The increase in CH₄ emissions due to restoration must be considered when land use strategies to reduce emissions are developed. Likewise, assessing the suitability of peatland restoration processes requires a better understanding of C processes and dynamics changed by the restoration. Previous studies have resulted in the development of a guide called the "North American Peatland Restoration Guide" (Quinty & Rochefort, 2003). Application of this strategy can result in the return of a plant community that is dominated by species characteristic of peatlands (Quinty & Rochefort, 2003). The new emerging plant community, and altered hydrology resulting from restoration, should help to return GHG dynamics to those more similar to natural peatlands. In addition to producing high CH₄ emissions, rewetting also increases the dissolved organic carbon (DOC) and thereby the amount of DOC lost to rivers (Dawson & Smith, 2007; Strack, 2008). However, it is still unknown how much is eventually lost to the atmosphere in the form of CO₂. Thus, to have a clear picture of the advantages/disadvantages of restoration to preserve C stocks of northern peatlands, long-term investigations on the overall greenhouse gas balance are of great importance.

Future sustainable and climate-friendly management strategies are needed. These management practices should focus on preventing peatland degradation. Targets of climate protection on managed peatlands could be met by converting arable land to grassland, decreasing land-use intensity, and re-establishing the original ground WT (Byrne, Chojnicki, Christensen, Drösler, & Freibauer, 2004; Freibauer, Rounsevell, Smith, & Verhagen, 2004). Petrescu et al. (2015) reported that intensity of land management (e.g., conversion of natural peatlands to agricultural land) can strongly influence net climate footprint of wetlands and could eventually result in positive radiative forcing. They suggested that estimates of future releases of GHG inventories based on IPCC guidelines for wetlands should consider the relationship between CH₄ and CO₂ fluxes, the intensity of management, and the land use/land cover change on both the net GHG balance and thereby radiative forcing.

5 | CONCLUSIONS

In this review, we investigated the factors that control CH₄ emissions and impacts of management in northern peatlands (latitude 40° to 70°N). The study covered a total of 87 studies taken at 186 sites

covering different countries, peatland types, and management systems. We found CH₄ emissions from natural northern peatlands to be highly variable with a 95% CI of 7.6–15.7 g C m⁻² year⁻¹ for the mean and 3.3–6.3 g C m⁻² year⁻¹ for the median and an overall annual average (mean ± SD) of 12 ± 21 g C m⁻² year⁻¹. Compared to bogs, fens emit the highest levels of CH₄ to the atmosphere. The factors controlling the emissions are water table (WT) depth, plant community composition, and soil pH with an interaction with mean annual air temperature, indicating that maximum emissions occurs when MAAT ~ 2°C. Drainage significantly ($p < .05$) reduces the emissions, on average, by 84%, while rewetting of drained peatlands increases the emissions, on average, by 46%. Complex interactions between temperature and the other environmental variables determine CH₄ emissions from northern peatlands.

ACKNOWLEDGMENTS

This work was funded in part by the GHG-Europe Project (EU grant agreement number: 244122).

FUNDING INFORMATION

Greenhouse gases Europe project (Grant/Award Number: “244122”).

CONFLICT OF INTEREST

None declared.

REFERENCES

- Adams, G., Buteau, P., Dignard, N., Grondin, P., Jeglum, J., Keys, D., ... Zoltai, S. (1997). *The Canadian wetland classification system*. Second eds. Waterloo, ON: Wetlands Research Centre, University of Waterloo. ISBN: 0-662-25857-6. Accessed on the 12th of June 2016.
- Aerts, R., & Ludwig, F. (1997). Water-table changes and nutritional status affect trace gas emissions from laboratory columns of peatland soils. *Soil Biology and Biochemistry*, 29, 1691–1698.
- Aerts, R., Verhoeven, J. T. A., & Whigham, D. F. (1999). Plant-mediated controls on nutrient cycling in temperate fens and bogs. *Ecology*, 80, 2170–2181.
- Akima, H., & Gebhardt, A. (2015). Akima: Interpolation of Irregularly and Regularly Spaced Data. R package version 0.5-12. Retrieved from <http://CRAN.R-project.org/package=akima>.
- Alm, J., Saarnio, S., Nykänen, H., Silvola, J., & Martikainen, P. (1999). Winter CO₂, CH₄, and N₂O fluxes on some boreal natural and drained peatlands. *Biogeochemistry*, 44, 163–186.
- Bäckstrand, K., Crill, P. M., Jackowicz-Korczynski, M., Mastepanov, M., Christensen, T. R., & Bastviken, D. (2010). Annual carbon gas budget for a subarctic peatland, Northern Sweden. *Biogeochemistry*, 7, 95–108.
- Bain, P. G., Hornsey, M. J., Bongiorno, R., & Jeffries, C. (2012). Promoting pro-environmental action in climate change deniers. *Nature Climate Change*, 2, 603. doi:10.1038/nclimate1636
- Baird, A. J., Beckwith, C. W., Waldron, S., & Waddington, J. M. (2004). Ebullition of methane-containing gas bubbles from near-surface Sphagnum peat. *Geophysical Research Letter*, 31, L21505.
- Baird, A. J., Belyea, L., & Morris, P. J. (2009). Upscaling peatland-atmosphere fluxes of carbon gases: Small-scale heterogeneity in process rates and the pitfalls of ‘bucket-and-slab’ models. In A. J. Baird, L. R. Belyea, X. Comas, A. Reeve & L. Slater (Eds.), (2008) *Northern Peatlands and carbon cycling* (pp. 37–53). Washington, DC: American Geophysical Union Monograph. doi: 10.1029/2008GM000826
- Baird, A. J., Holden, J., & Chapman, P. J. (2009). A literature Review of Evidence on Emissions of Methane in Peatlands. Defra Project SP0574. Retrieved from <http://randd.defra.gov.uk/Default.aspx?Menu=Menu&Module=More&Location=None&Completed=0&ProjectID=15992>.
- Basiliko, N., Knowles, R., & Moore, T. R. (2004). Roles of moss species and habitats in methane consumption potential in a northern peatland. *Wetlands*, 24, 178–185.
- Basiliko, N., Yavitt, J. B., Dees, P. M., & Merkel, S. M. (2003). Methane biogeochemistry and methanogen communities in two northern peatland ecosystems, New York State. *Geomicrobiology Journal*, 20, 563–577.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. Retrieved from <http://cran.r-project.org/package=lme4>
- Beetz, S., Liebersbach, H., Glatzel, S., Jurasinski, G., Buczo, U., & Höper, H. (2013). Effects of land use intensity on the full greenhouse gas balance in an Atlantic peat bog. *Biogeochemistry*, 10, 1067–1082.
- Belisario, L. M., Bubier, J. L., & Moore, T. R. (1999). Controls on CH₄ emissions from a northern peatland. *Global Biogeochemical Cycles*, 13, 81–91.
- Belyea, L. R., & Clymo, R. (2001). Feedback control of the rate of peat formation. *Proceedings of the Royal Society of London*, 268, 1315–1321.
- Bergman, I., Svensson, B. H., & Nilsson, M. (1998). Regulation of methane production in a Swedish acid mire by pH, temperature and substrate. *Soil Biology and Biochemistry*, 30, 729–741.
- Bergman, I., Klarqvist, M., & Nilsson, M. (2000). Seasonal variation in rates of methane production from peat of various botanical origins: Effects of temperature and substrate quality. *FEMS Microbiology Ecology*, 33, 181–189.
- Beyer, C., & Höper, H. (2015). Greenhouse gas exchange of rewetted bog peat extraction sites and a Sphagnum cultivation site in northwest Germany. *Biogeochemistry*, 12, 2101–2117.
- Beyer, C., Liebersbach, H., & Höper, H. (2015). Multiyear greenhouse gas flux measurements on a temperate fen soil used for cropland or grassland. *Journal of Plant Nutrition and Soil Science*, 178, 99–111.
- Bodelier, P. L. E., & Laanbroek, H. J. (2004). Nitrogen as a regulatory factor of methane oxidation in soils and sediments. *FEMS Microbiology Ecology*, 47, 265–277.
- Bridgman, S. D., Cadillo-Quiroz, H., Keller, J. K., & Zhuang, Q. (2013). Methane emissions from wetlands: Biogeochemical, microbial, and modeling perspectives from local to global scales. *Global Change Biology*, 19, 1325–1346.
- Brown, M. G., Humphreys, E. R., Moore, T. R., Roulet, N. T., & Lafleur, P. M. (2014). Evidence for a nonmonotonic relationship between ecosystem-scale peatland methane emissions and water table depth. *Journal of Geophysical Research Biogeochemistry*, 119, 826–835.
- Bruhwiller, L., Dlugokencky, E., Masarie, K., Ishizawa, M., Andrews, A., Miller, J., ... Worthy, D. (2014). Carbontracker-CH₄: An assimilation system for estimating emissions of atmospheric methane. *Atmospheric Chemistry and Physics*, 14, 8269–8293.
- Bubier, J. L. (1995). The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. *Journal of Ecology*, 83, 403–420.
- Bubier, J. L., Moore, T. R., & Roulet, N. T. (1993). M methane emissions from wetlands in the midboreal region of northern Ontario, Canada. *Ecology*, 74, 2240–2254.
- Bussell, J., Jones, D. L., Healey, J. R., & Pullin, A. S. (2012). How do draining and re-wetting affect carbon stores and greenhouse gas fluxes in peatland soils? CEE review 08-012 (SR49). Collaboration for Environmental Evidence: Accessed in June 2014. Retrieved from www.environmentalevidence.org/SR49.html
- Byrne, K. A., Chojnicki, B., Christensen, T. R., Drösler, M., & Freibauer, A. (2004). EU peatlands: Current carbon stocks and trace gas fluxes. CarboEurope-GHG Concerted Action – Synthesis of the European

- Greenhouse Gas Budget, Report 4/2004, Specific Study, Tipo-Lito Recchioni, Viterbo, October 2004, ISSN 1723-2236.
- Carter, S., Sutton, A., & Stenglen, R. M. (2012). Diet and feed management to mitigate airborne emissions. *Air Quality Education in Animal Agriculture*, pp. 10. Accessed in June 2014. Retrieved from <http://articles.extension.org/sites/default/files/Dietand%20Feed%20FINAL.pdf>
- Castaldi, S., Ermice, A., & Strumia, S. (2006). Fluxes of N_2O and CH_4 from soils of savannas and seasonally-dry ecosystems. *Journal of Biogeography*, 33, 401–415.
- Christensen, T. R., Ekberg, A., Ström, L., Mastepanov, M., Panikov, N., Öquist, M., ... Oskarsson, H. (2003). Factors controlling large scale variations in methane emissions from wetlands. *Geophysical Research Letter*, 30, 1414, doi: 10.1029/2002GL016848.
- Christensen, T. R., Friborg, T., & Sommerkorn, M. (2000). Trace gas exchange in a high arctic valley 1: Variations in CO_2 and CH_4 flux between tundra vegetation types. *Global Biogeochemical Cycles*, 14, 701–714.
- Ciais, P., Sabine, C., Govindasamy, B., Bopp, L., Brovkin, V., Canadell, J., ... Thornton, P. (2013). Chapter 6. Carbon and Other. Biogeochemical Cycles. In T. Stocker, D. Qin, & G. X. K. Plattner (Eds.), *Climate change 2013. The physical science basis* (pp. 465–570). Cambridge: Cambridge University Press.
- Clymo, R. S. (1983). Peat. In: A. J. P. Gore (Ed.), *Mires: Swamp, bog, fen, and moor (Ecosystems of the world 4A)* (pp. 159–224). Amsterdam: Elsevier.
- Conrad, R. (1996). Soil microorganisms as controllers of atmospheric trace gases (H_2 , CO , CH_4 , OCS , N_2O , and NO). *Microbiological Reviews*, 60, 609–640.
- Cooper, M. D. A., Evans, C. D., Zielinski, P., Levy, P. E., Gray, A., Peacock, M., ... Freeman, C. (2014). Infilled ditches are hotspots of landscape methane flux following peatland re-wetting. *Ecosystems*, 17, 1227–1241.
- Couwenberg, J., & Fritz, C. (2012). Towards developing IPCC methane 'emission factors' for peatlands (organic soils). *Mires and Peat*, 10, 1–17.
- Crill, P. M., Bartlett, K. B., Harriss, R. C., Gorham, E., Verry, E. S., Sebach, D. I., ... Sanner, W. (1988). Methane flux from Minnesota peatlands. *Global Biogeochemical Cycles*, 2, 371–384.
- Dalva, M., & Moore, T. R. (2001). Methane and soil and plant community respiration from wetlands, Kejimikujik National Park, Nova Scotia: Measurements predictions and climatic change. *Journal of Geophysical Research*, 106(D3), 2955–2962.
- Danevcic, T., Mandic-Mulec, I., Stres, B., Stopar, D., & Hacin, J. (2010). Emissions of CO_2 , CH_4 and N_2O from Southern European peatlands. *Soil Biology and Biochemistry*, 42, 1437–1446.
- Dawson, J. J. C., & Smith, P. (2007). Carbon losses from soil and its consequences for land management. *Science of the Total Environment*, 382, 165–190.
- Denman, K. L., Brasseur, G., Chidthaisong, A., Ciais, P., Cox, P. M., Dickinson, R. E., ... Zhang, X. (2007). Couplings Between Changes in the Climate System and Biogeochemistry. In S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, ... H. L. Miller (Eds.), *Climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change* (pp. 449–587). Cambridge, UK and New York, NY: Cambridge University Press.
- Desai, A. R., Xu, K., Tian, H., Weishampel, P., Thom, J., Baumann, D., ... Kolka, R. (2015). Landscape-level terrestrial methane flux observed from a very tall tower. *Agricultural and Forest Meteorology*, 201, 61–75.
- Ding, W. X., & Cai, Z. C. (2007). Methane emission from natural wetlands in China: Summary of years 1995–2004 studies. *Pedosphere*, 17, 475–485.
- Dinsmore, K. J., Skiba, U. M., Billett, M. F., & Rees, R. M. (2009). Effect of water table on greenhouse gas emissions from peatland mesocosms. *Plant and Soil*, 318, 229–242.
- Dise, N. B., Gorham, E., & Verry, E. S. (1993). Environmental factors controlling methane emissions from peatlands in Northern Minnesota. *Journal of Geophysical Research*, 98, 583–594.
- Drewer, J., Lohila, A., Aurela, M., Laurila, T., Minkinen, K., Penttilä, T., ... Skiba, U. M. (2010). Comparison of greenhouse gas fluxes and nitrogen budgets from an ombrotrophic bog in Scotland and a minerotrophic sedge fen in Finland. *European Journal of Soil Science*, 61, 640–650.
- Evans, C. D., Monteith, D. T., & Cooper, D. M. (2005). Long-term increases in surface water dissolved organic carbon: Observations, possible causes and environmental impacts. *Environmental Pollution*, 137(1), 55–71.
- FAO (2008). Food and Agriculture Organization of the United Nations. European Forestry Commission. Working party on the management of mountain water sheds. Final Report, Oulu, Finland, 19–22 August.
- Forster, P., Ramaswamy, V., Artaxo, P., Bernsten, T., Betts, R., Fahey, D. W., ... Van Dorland, R. (2007). Changes in Atmospheric Constituents and in Radiative Forcing. In S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, ... H. L. Miller (Eds.), *Climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change* (pp. 131–217). Cambridge, UK and New York, NY: Cambridge University Press.
- Freibauer, A., Rounsevell, M., Smith, P., & Verhagen, A. (2004). Carbon sequestration in the agricultural soils of Europe. *Geoderma*, 122, 1–23.
- Frenzel, P., & Karofeld, E. (2000). CH_4 emission from a hollow-ridge complex in a raised bog: The role of CH_4 production and oxidation. *Biogeochemistry*, 51, 91–112.
- Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., ... Zeng, N. (2006). Climate-carbon cycle feedback analysis: Results from the C4MIP model intercomparison. *Journal of Climate*, 19, 3337–3353.
- Frolking, S., Talbot, J., Jones, M. C., Treat, C. C., Kauffman, J. B., Tuittila, E.-S., & Roulet, N. (2011). Peatlands in the Earth's century climate system. *Environmental Reviews*, 19, 371–395.
- Gedney, N., Cox, P. M., & Huntingford, C. (2004). Climate feedback from wetland methane emissions. *Geophysical Research Letters*, 31, L20503.
- Glaser, P. H., Chanton, J. P., Morin, P., Rosenberry, D. O., Siegel, D. I., Ruud, O., Chasar, L. I., & Reeve, A. S. (2004). Surface deformations as indicators of deep ebullition fluxes in a large northern peatland. *Global Biogeochemical Cycles*, 18, GB1003.
- Glenn, S., Heyes, A., & Moore, T. (1993). Carbon dioxide and methane fluxes from drained peat soils, southern Quebec. *Global Biogeochemical Cycles*, 7, 247–257.
- Godin, A., McLaughlin, J. W., Webster, K. L., Packalen, M., & Basiliko, N. (2012). Methane and methanogen community dynamics across a boreal peatland nutrient gradient. *Soil Biology and Biochemistry*, 48, 96–105.
- Graf, M. D., Rochefort, L., & Poulin, M. (2008). Spontaneous revegetation of cutaway peatlands of North America. *Wetlands*, 28, 28–39.
- Granberg, G., Mikkilä, C., Sundh, I., Svensson, B. H., & Nilsson, M. (1997). Source of spatial variation in methane emission from mires in northern Sweden: A mechanistic approach in statistical modeling. *Global Biogeochemical Cycles*, 11, 135–150.
- Granberg, G., Sundh, I., Svensson, B. H., & Nilsson, M. (2001). Effects of temperature, and nitrogen and sulfur deposition, on methane emission from a boreal mire. *Ecology*, 82, 1982–1998.
- Greenup, A. L., Bradford, M. A., McNamara, N. P., Ineson, P., & Lee, J. A. (2000). The role of *Eriophorum vaginatum* in CH_4 flux from an ombrotrophic peatland. *Plant and Soil*, 227, 265–272.
- Hahn-Schoff, M., Zak, D., Minke, M., Gelbrecht, J., Augustin, J., & Freibauer, A. (2011). Organic sediment formed during inundation of a degraded fen grassland emits large fluxes of CH_4 and CO_2 . *Biogeosciences*, 8, 1539–1550.
- Hanis, K. L., Tenuta, M., Amiro, B. D., & Papakyriakou, T. N. (2013). Seasonal dynamics of methane emissions from a subarctic fen in the Hudson Bay Lowlands. *Biogeosciences*, 10, 4465–4479.
- Hanson, R. S., & Hanson, T. E. (1996). Methanotrophic bacteria. *Microbiological Reviews*, 60, 439–471.
- Hargreaves, K. J., & Fowler, D. (1998). Quantifying the effects of soil temperature and water table on the emission of methane from peat wetland at the field scale. *Atmospheric Environment*, 32, 3275–3282.

- Hargreaves, K. J., Fowler, D., Pitcairn, C. E. R., & Aurela, M. (2001). Annual methane emission from Finnish mires estimated from eddy covariance campaign measurements. *Theoretical and Applied Climatology*, 70, 203–213.
- Hendriks, D. M. D., van Huissteden, J., Dolman, A. J., & van der Molen, M. K. (2007). The full greenhouse gas balance of an abandoned peat meadow. *Biogeosciences*, 4, 411–424.
- Henneberg, A., Elsgaard, L., Sorrell, B. K., Brix, H., & Petersen, S. O. (2015). Does *Juncus effusus* enhance methane emissions from grazed pastures on peat? *Biogeosciences*, 12, 5667–5676.
- Hillman, P., Gerbamedhin, K., & Warner, R. (1992). Ventilation system to minimize airborne bacteria, dust, humidity, and ammonia in calf nurseries. *Journal of Dairy Science*, 75, 1305–1312.
- Holden, J. (2005). Peatland hydrology and carbon cycling: Why small scale process matters. *Philosophical Transactions of the Royal Society A*, 363, 2891–2913.
- Holden, J., Shotbolt, L., Bonn, A., Burt, T. P., Chapman, P. J., Dougill, A. J., ... Worrall, F. (2007). Environmental change in moorland landscapes. *Earth Science Reviews*, 82, 75–100.
- Hou, A. X., Wang, Z. P., Chen, G. X., & Patrick, W. H. (2000). Effects of organic and N fertilizers on methane production potential in a Chinese rice soil and its microbiological aspect. *Nutrient Cycling Agroecosystems*, 58, 33–338.
- Hutchins, B. W. (1998). Tillage and land use effects on methane oxidation rates and their vertical profiles in soil. *Biology and Fertility of Soils*. New York, 27(3), 284–292.
- Huttunen, J. T., Nykänen, H., Turunen, J., & Martikainen, P. J. (2003). Methane emissions from natural peatlands in the northern boreal zone in Finland. *Fennoscandia Atmospheric Environment*, 37, 147–151.
- IPCC (2013). Summary for Policymakers. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, ... P. M. Midgley (Eds.), *Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change* (pp. 1535). Cambridge, UK and New York, NY, USA: Cambridge University Press.
- Jackowicz-Korczynski, M., Christensen, T. R., Bäckstrand, K., Crill, P., Friborg, T., Mastepanov, M., & Strom, L. (2010). Annual cycle of methane emission from a subarctic peatland. *Journal of Geophysical Research-Biogeosciences*, 115(G2), pp. 10.
- Joabsson, A., Christensen, T. R., & Walle'n, B. (1999). Vascular plant controls on methane emissions from northern peatforming wetlands. *Trends in Ecology and Evolution*, 14, 385–388.
- Josse, J., & Husson, F. (2016). missMDA: A package for handling missing values in multivariate data analysis. *Journal of Statistical Software*, 70(1), 1–31. doi:10.18637/jss.v070.i01
- Juottonen, H., Galand, P. E., Tuittila, E. S., Laine, J., Fritze, H., & Yrjälä, K. (2005). Methanogen communities and bacteria along an ecophysiological gradient in a northern raised bog complex. *Environmental Microbiology*, 7, 1547–1557.
- Juottonen, H., Hynninen, A., Nieminen, M., Tuomivirta, T., Tuittila, E. S., Noutsainen, H., ... Fritze, H. (2012). Methane-cycling microbial communities and methane emission in natural and restored peatlands. *Applied and Environmental Microbiology*, 78, 6386–6389.
- Juszczak, R., & Augustin, J. (2013). Exchange of the greenhouse gases methane and nitrous oxide between the atmosphere and a temperate peatland in central Europe. *Wetlands*, 33, 895–907.
- Kimmel, K., & Mander, Ü. (2010). Ecosystem services of peatlands: Implications for restoration. *Progress in Physical Geography*, 34, 491–514.
- King, J. Y., Reeburgh, W. S., & Regli, S. K. (1998). Methane emission and transport by arctic sedges in Alaska: Results of a vegetation removal experiment. *Journal of Geophysical Research*, 103, 29083–29092.
- Kirschbaum, M. U. F. (1995). The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biology and Biochemistry*, 27, 753–760.
- Kirschke, S., Bousquet, P., Ciais, P., Saunio, M., Canadell, J. G., Dlugokencky, E. J., ... Blake, D. R. (2013). Three decades of global methane sources and sinks. *Nature Geoscience*, 6, 813–823.
- Komulainen, V. M., Nykänen, H., Martikainen, P. J., & Laine, J. (1998). Short-term effect of restoration on vegetation change and methane emissions from peatlands drained for forestry in southern Finland. *Canadian Journal of Forest Research*, 28(3), 402–411.
- Kuznetsova, A., Brockhoff, P. B., & Bojesen Christensen, R. H. (2013). lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). Retrieved from <http://cran.r-project.org/package=lmerTest>
- Lai, D. Y. F. (2009). Methane dynamics in northern peatlands: A review. *Pedosphere*, 19(4), 409–421.
- Lai, D. Y. F., Moore, T. R., & Roulet, N. T. (2014). Spatial and temporal variations of methane flux measured by autochambers in a temperate ombrotrophic peatland. *Journal of Geophysical Research Biogeosciences*, 119, 864–880.
- Laine, J., Vasander, H., & Laiho, R. (1995). Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. *Journal of Applied Ecology*, 32, 785–802.
- Laine, A., Wilson, D., Kiely, G., & Byrne, K. A. (2007). Methane flux dynamics in an Irish lowland blanket bog. *Plant and Soil*, 299, 181–193.
- Le Mer, J., & Rodger, P. (2001). Production, oxidation, emission and consumption of methane by soils: A review. *European Journal Soil Biology*, 37, 25–50.
- Lefcheck, J. S. (2016). PIECEWISESEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7, 573–579.
- Levy, P., Burden, A., Cooper, M. D. A., Dinsmore, K. J., Drewer, J., Evans, C., ... Zielinski, P. (2012). Methane emissions from soils: Synthesis and analysis of a large UK data set. *Global Change Biology*, 18, 1657–1669.
- Liblik, L. K., Moore, T. R., Bubier, J. L., & Robinson, S. D. (1997). Methane emissions from wetlands in the zone of discontinuous permafrost: Fort Simpson, Northwest Territories, Canada. *Global Biogeochemical Cycles*, 11, 485–494.
- Lohila, A., Minkinen, K., Aurela, M., Tuovinen, J.-P., Penttilä, T., Ojanen, P., & Laurila, T. (2011). Greenhouse gas flux measurements in a forestry-drained peatland indicate a large carbon sink. *Biogeosciences*, 8, 3203–3218.
- Loisel, J., Yu, Z., Beilman, D. W., Camill, P., Alm, J., Amesbury, M. J., ... Bochicchio, C. (2014). A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. *The Holocene*, 24, 1028–1042.
- Long, K., Flanagan, L. B., & Cai, T. O. (2010). Diurnal and seasonal variation in methane emissions in a northern Canadian peatland measured by eddy covariance. *Global Change Biology*, 16, 2420–2435.
- Lund, M., Christensen, T. R., Mastepanov, M., Lindroth, A., & Strom, L. (2009). Effects of N and P fertilization on the greenhouse gas exchange in two northern peatlands with contrasting N deposition rates. *Biogeosciences*, 6, 2135–2144.
- Mahmood, M. D. S., & Strack, M. (2011). Methane dynamics of recolonized cutover minerotrophic peatland: Implications for restoration. *Ecological Engineering*, 37, 1859–1868.
- Mäkiranta, P., Hytönen, J., Aro, L., Maljanen, M., Pihlatie, M., Potila, H., ... Minkinen, K. (2007). Soil greenhouse gas emissions from afforested organic soilcroplands and cutaway peatlands. *Boreal Environment Research*, 12, 159–175.
- Maljanen, M., Hytönen, J., & Martikainen, P. J. (2001). Fluxes of N₂O, CH₄ and CO₂ on afforested boreal agricultural soils. *Plant and Soil*, 231, 113–121.
- Maljanen, M., Sigurdsson, B. D., Gudmundsson, J., Oskarsson, H., Huttunen, J. T., & Martikainen, P. J. (2010). Greenhouse gas balances of managed peatlands in the Nordic countries -present knowledge and gaps. *Biogeosciences*, 7, 2711–2738.
- Mander, Ü., Järveoja, J., Maddison, M., Soosaar, K., Aavola, R., Ostonen, K., & Salm, J. (2012). Reed canary grass cultivation mitigates greenhouse gas emissions from abandoned peat extraction areas. *GCB Bioenergy*, 4, 462–474.

- Mastepanov, M., Sigsgaard, C., Tagesson, T., Ström, L., Tamstorf, M. P., Lund, M., & Christensen, T. R. (2013). Revisiting factors controlling methane emissions from high-Arctic tundra. *Biogeosciences*, 10, 5139–5158.
- McCalley, C. K., Woodcroft, B. J., Hodgkins, S. B., Wehr, R. A., Kim, E. H., Mondav, R., ... Saleska, S. R. (2014). Methane dynamics regulated by microbial community response to permafrost thaw. *Nature*, 514, 478–481.
- McNamara, N. P., Plant, T., Oakley, S., & Ostle, N. J. (2008). Gully hotspot contribution to landscape methane and carbon dioxide fluxes in a northern peatland. *Science of the Total Environment*, 404, 354–360.
- Minkinen, K., Byrne, K. A., & Trettin, C. (2008). Climate impacts of peatland forestry. In M. Strack (Ed.), *Peatlands and climate change* (pp. 98–122). Jyväskylä, Finland: International Peat Society.
- Minkinen, K., Korhonen, R., Savolainen, I., & Laine, J. (2002). Carbon balance and radiative forcing of Finnish peatlands 1900–2100 – the impact of forestry drainage. *Global Change Biology*, 8, 785–799.
- Minkinen, K., & Laine, J. (2006). Vegetation heterogeneity and ditches create spatial variability in methane fluxes from peatlands drained for forestry. *Plant and Soil*, 285, 289–304.
- Minkinen, K., Laine, J., Nykänen, H., & Martikainen, P. J. (1997). Importance of drainage ditches in emissions of methane from mires drained for forestry. *Canadian Journal of Forest Research*, 27, 949–952.
- Mitsch, W. J., Bernal, B., Nahlik, A. M., Mander, Ü., Zhang, L., Anderson, L., ... Brix, H. (2013). Wetlands, carbon, and climate change. *Landscape Ecology*, 28(4), 583–597.
- Mojeremane, W., Rees, R. M., & Mencuccini, M. (2010). Effects of site preparation for afforestation on methane fluxes at Harwood Forest, NE England. *Biogeochemistry*, 97, 89–107.
- Moore, T. R., & Dalva, M. (2006). The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. *Journal of Soil Science*, 44, 651–664.
- Moore, T. R., & Knowles, R. (1989). The influence of water table levels on methane and carbon dioxide emissions from peatland soils. *Canadian Journal of Soil Science*, 69, 33–38.
- Moore, T. R., De Young, A., Bubier, J. L., Humphreys, E. R., Lafleur, P. M., & Roulet, N. T. (2011). A multi-year record of methane flux at the Mer Bleue Bog, southern Canada. *Ecosystems*, 14, 646–657.
- Nadeau, D. F., Rousseau, A. N., Coursole, C., Margolis, H. A., & Parlange, M. B. (2013). Summer methane fluxes from a boreal bog in northern Quebec, Canada, using eddy covariance measurements. *Atmospheric Environment*, 81, 464–474.
- Nilsson, M., Mikkilä, C., Sundh, I., Granberg, G., Svensson, B. H., & Ranneby, B. (2001). Methane emission from Swedish mires: National and regional budgets and dependence on mire vegetation. *Journal of Geophysical Research*, 106, 20847–20860.
- Nilsson, M., Sagerfors, J., Buffam, I., Laudon, H., Eriksson, T., Grelle, A., ... Lindroth, A. (2008). Contemporary carbon accumulation in boreal oligotrophic minerogenic mire—a significant sink after accounting for all C-fluxes. *Global Change Biology*, 14, 2317–2332.
- Nykänen, H., Alm, J., Lang, K., Silvola, J., & Martikainen, P. J. (1995). Emissions of CH₄, N₂O and CO₂ from a virgin fen and a fen drained for grassland in Finland. *Journal of Biogeography*, 22, 351–357.
- Nykänen, H., Alm, J., Silvola, J., Tolonen, K., & Martikainen, P. J. (1998). Methane fluxes on boreal peatlands of different fertility and the effect of long-term experimental lowering of the water table on flux rates. *Global Biogeochemical Cycles*, 12, 53–69.
- Nykänen, H., Heikkinen, J. E. P., Pirinen, L., Tiilikainen, K., & Martikainen, P. J. (2003). Annual CO₂ exchange and CH₄ fluxes on a subarctic palsamire during climatically different years. *Global Biogeochemical Cycles*, 17, 1018.
- Olefelt, D., Roulet, N. T., Bergeron, O., Crill, P., Bäckstrand, K., & Christensen, T. R. (2012). Net carbon accumulation of a high-latitude permafrost palsamire similar to permafrost-free peatlands. *Geophysics Research Letter*, 39, L03501.
- Olefelt, D., Turetsky, M. R., Crill, P. M., & McGuire, A. D. (2013). Environmental and physical controls on northern terrestrial methane emissions across permafrost zones. *Global Change Biology*, 19, 589–603.
- Oleszczuk, R., Regina, K., Szajdak, H., Höper, H., & Maryga-nova, V. (2008). Impacts of agricultural utilization of peat soils on the greenhouse gas balance. In M. Strack (Ed.), *Peatlands and climate change* (pp. 70–97). Jyväskylä, Finland: International Peat Society.
- Olson, D. M., Griffis, T. J., Noormets, A., Kolka, R., & Chen, J. (2013). Interannual, seasonal, and retrospective analysis of the methane and carbon dioxide budgets of a temperate peatland. *Journal of Geophysical Research: Biogeosciences*, 118, 226–238.
- Panikov, N. S., & Dedysh, S. N. (2000). Cold season CH₄ and CO₂ emission from boreal peat bogs (West Siberia): Winter fluxes and thaw activation dynamics. *Global Biogeochemical Cycles*, 14, 1071–1080.
- Pelletier, L., Moore, T. R., Roulet, N. T., Garneau, M., & Beaulieu-Audy, V. (2007). Methane fluxes from three peatlands in the La Grande Rivière watershed, James Bay lowland, Canada. *Journal of Geophysical Research*, 112, G01018.
- Petrescu, A. M. R., Lohila, A., Tuovinen, J. P., Baldocchi, D. D., Desai, A. R., Roulet, N. T., ... Cescatti, A. (2015). The uncertain climate footprint of wetlands under human pressure. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 4594–4599.
- Petrone, R. M., Price, J. S., Waddington, J. M., & von Waldow, H. (2004). Surface moisture and energy exchange from a restored peatland, Quebec, Canada. *Journal of Hydrology*, 295, 198–210.
- Prevost, M., Belleau, P., & Plamondon, A. P. (1997). Substrate conditions in a treed peatland: Response to drainage. *Ecoscience*, 4(4), 543–554.
- Price, J. S., & Ketcheson, S. J. (2009). Water relations in cutover peatlands. In A. Baird, L. Belyea, X. Comas, A. Reeve, & L. Slater (Eds.), *Carbon cycling in Northern Peatlands*. *Geophysical monograph series*, 184 (pp. 277–287).
- Pypker, T. G., Moore, P. A., Waddington, J. M., Hribljan, J. A., & Chimner, R. C. (2013). Shifting environmental controls on CH₄ fluxes in a sub-boreal peatland. *Biogeosciences*, 10, 7971–7981.
- Quinty, F., & Rochefort, L. (2003). *Peatland restoration guide*, 2nd edn. Québec, Canada: Canadian Sphagnum Peat Moss Association and New Brunswick Department of Natural Resources and Energy. Accessed in July 2014. Retrieved from http://tourbehorticole.com/wp-content/uploads/2015/07/Peatland_Restoration-e.pdf
- R Development Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.r-project.org/>
- Raghoebarsing, A. A., Smolders, A. J. P., Schmid, M. C., Rijpstra, W. I. C., Wolters-Arts, M., Derksen, J., ... Strous, M. (2005). Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. *Nature*, 436, 1153–1156.
- Reeburg, W. S., Whalen, S. C., & Alperin, M. J. (1993). The role of methanotrophy in the global methane budget. In J. C. Murrell & D. P. Kelly (Eds.), *Microbial growth on C1 compounds* (pp. 1–14). Andover, UK: Intercept.
- Rinne, J., Riutta, T., Pihlatie, M., Aurela, M., Haapanala, S., Tuovinen, J. P., ... Vesala, T. (2007). Annual cycle of methane emission from a boreal fen measured by the eddy covariance technique. *Tellus*, B 59, 449–457.
- Rosenberry, D. O., Glaser, P. H., Siegel, D. I., & Weeks, E. D. (2003). Use of hydraulic head to estimate volumetric gas content and ebullition flux in northern peatlands. *Water Resources Research*, 39(3), 1066.
- Roulet, N. T., Ash, R., & Quinton, W. (1993). Methane flux from drained northern peatlands: Effect of a persistent water table lowering on flux. *Global Biogeochemical Cycles*, 7, 749–769.
- Roulet, N. T., Jano, A., Kelly, C. A., Klinger, L. F., Moore, T. R., Protz, R., ... Rouse, W. R. (1994). Role of the Hudson Bay lowland as a source of atmospheric methane. *Journal of Geophysical Research*, 99, 1439–1454.

- Roulet, N. T., Lafleur, P. M., Richard, P. J. H., Moore, T. R., Humphreys, E. R., & Bubier, J. (2007). Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland. *Global Change Biology*, 13, 397–411.
- Roulet, N. T., & Moore, T. R. (1995). The effect of forestry drainage practices on the emission of methane from northern peatlands. *Canadian Journal of Forest Research*, 25, 491–499.
- Roulet, N. T., Ash, R., & Moore, T. R. (1992). Low boreal wetlands as a source of atmospheric methane. *Journal of Geophysical Research*, 97, 3739–3749.
- Rydin, H., & Jeglum, J. (2006). *The biology of Peatlands*. New York, NY: Oxford University Press.
- Saarnio, S., Alm, J., Martikainen, P. J., & Silvola, J. (1998). Effects of raised CO₂ on potential CH₄ production and oxidation in, and CH₄ emission from, a boreal mire. *Journal of Ecology*, 86, 261–268.
- Saarnio, S., Winiwarter, W., & Leitaio, J. (2009). Methane release from wetlands and watercourses in Europe. *Atmospheric Environment*, 43, 1421–1429.
- Saarnio, S., Morero, M., Shurpali, N., Tuittila, E. S., Makila, M., & Alm, J. (2007). Annual CO₂ and CH₄ fluxes of pristine boreal mires as a background for the lifecycle analyses of peat energy. *Boreal Environment Research*, 12, 101–113.
- Salm, J., Maddison, M., Tammik, S., Soosaar, K., Truu, J., & Mander, Ü. (2012). Emissions of CO₂, CH₄ and N₂O from undisturbed, drained and mined peatlands in Estonia. *Hydrobiologia*, 692, 41–55.
- Samaritani, E., Siegenthaler, A., Yli-Petäys, M., Buttler, A., Christin, P., & Mitchell, E. A. D. (2011). Seasonal net ecosystem carbon exchange of a regenerating cutaway bog: How long does it take to restore the C-sequestration function? *Restoration Ecology*, 19, 480–489.
- Schrier-Uijl, A. P., Veenendaal, E. M., Leffelaar, P. A., van Huissteden, J. C., & Berendse, F. (2010). Methane emissions in two drained peat agroecosystems with high and low agricultural intensity. *Plant and Soil*, 329, 509–520.
- Seghers, D., Top, E. M., Reheul, D., Bulcke, R., Boeckx, P., Verstraete, W., & Siciliano, S. D. (2003). Long-term effects of mineral versus organic fertilizers on activity and structure of the methanotrophic community in agricultural soils. *Environmental Microbiology*, 5, 867–877.
- Shannon, R. D., & White, J. R. (1994). A three-year study of controls on methane emissions from two Michigan peatlands. *Biogeochemistry*, 27, 35–60.
- Singh, S., Singh, J. S., & Kashyap, A. K. (1999). Methane flux from irrigated rice fields in relation to crop growth and N-fertilization. *Soil Biology and Biochemistry*, 31, 1219–1228.
- Sirin, A., & Laine, J. (2008). Peatlands and greenhouse gases. In F. Parish (Ed.), *Assessment on peatlands, biodiversity and climate change* (pp. 118–138). Global Environment Centre, Kuala Lumpur and Wetlands International: Wageningen.
- Strack, M. (Ed.). (2008) Northern Peatlands, greenhouse gas exchange and climate change. In: Peatlands and climate change. University of Calgary, Canada. International Peat Society, 2008. Saarijärven Offset Oy, Saarijärvi, Finland.
- Strack, M., Waddington, J. M., & Tuittila, E. S. (2004). Effect of water table drawdown on northern peatland methane dynamics: Implications for climate change. *Global Biogeochemical Cycles*, 18, GB4003.
- Strack, M., & Zuback, Y. C. A. (2013). Annual carbon balance of a peatland 10 yr following restoration. *Biogeosciences*, 10, 2885–2896.
- Ström, L., Ekberg, A., Mastepanov, M., & Christensen, T. R. (2003). The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. *Global Change Biology*, 9, 1185–1192.
- Sundh, I., Mikkela, E. C., Nilsson, M., & Svensson, B. H. (1995). Potential aerobic methane oxidation in a Sphagnum-dominated peatland: Controlling factors and relation to methane emission. *Soil Biology and Biochemistry*, 27, 829–837.
- Sundh, I., Nilsson, M., Mikkela, C., Granberg, G., & Svensson, H. (2000). Fluxes of methane and carbon dioxide on peat-mining areas in Sweden. *Ambio*, 29, 499–503.
- Suyker, A. E., Verma, S. B., Clement, R. J., & Billesbach, D. P. (1996). Methane flux in boreal fen: Season-long measurement by eddy correlation. *Journal of Geophysical Research*, 101, 28637–28647.
- Tang, J., Miller, P. A., Persson, A., Olefeldt, D., Pilesjö, P., Heliasz, M., ... Christensen, T. R. (2015). Carbon budget estimation of a subarctic catchment using a dynamic ecosystem model at high spatial resolution. *Biogeosciences*, 12, 9721–2808.
- Tate, K. R., Ross, D. J., Saggat, S., Hedley, C. B., Dando, J., Singh, B. K., & Lambie, S. M. (2007). Methane uptake in soils from *Pinus radiata* plantations, a reverting shrubland and adjacent pastures: Effects of land-use change, and soil texture, water and mineral nitrogen. *Soil Biology and Biochemistry*, 39, 1437–1449.
- Tokida, T., Miyazaka, T., Mizoguchi, M., Nagata, O., Takakai, F., Kagemoto, A., & Natano, R. (2007). Falling atmospheric pressure as a trigger for methane ebullition from peatland. *Global Biogeochemical Cycles*, 21(2), pp. 8.
- Treat, C. C., Bubier, J. L., Varner, R. K., & Crill, P. M. (2007). Timescale dependence of environmental and plant-mediated controls on CH₄ flux in a temperate fen. *Journal of Geophysical Research*, 112, G01014.
- Trudeau, N. C., Garneau, M., & Pelletier, L. (2013). Methane fluxes from a patterned fen of the North eastern part of the La Grande river watershed, James Bay, Canada. *Biogeochemistry*, 113, 409–422.
- Tuittila, E. S., Komulainen, V. M., Vasander, H., Nykänen, H., Martikainen, P. J., & Laine, J. (2000). Methane dynamics of a restored cut-away peatland. *Global Change Biology*, 6, 569–581.
- Turetsky, M. R., Kotowska, A., Bubier, J., Dise, N., Nancy, B., Crill, P., ... Wilmking, M. (2014). A synthesis of methane emissions from 71 northern, temperate, and subtropical peatlands. *Global Change Biology*, 20, 2183–2197.
- Turetsky, M. R., Treat, C. C., Waldrop, M. P., Waddington, J. M., Harden, J. W., & McGuire, A. D. (2008). Short-term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland. *Journal of Geophysical Research*, 113, G00A10.
- Updegraff, K., Bridgman, S. D., Pastor, J., Weishampel, P., & Harth, C. (2001). Response of CO₂ and CH₄ emissions from peatlands to warming and water table manipulation. *Ecological Applications*, 11(2), 311–326.
- Urbanova, Z., Barta, J., & Picek, T. (2013). Methane emissions and methanogenic archaea on pristine, drained and restored mountain peatlands, Central Europe. *Ecosystems*, 16, 664–677.
- Urbanova, Z., Picek, T., & Tuittila, E. S. (2013). Sensitivity of carbon gas fluxes to weather variability on pristine, drained and rewetted temperate bogs. *Mires and Peat*, 11, 1–14.
- Vanselow-Algan, M., Schmidt, S. R., Greven, M., Fiencke, C., Kutzbach, L., & Pfeiffer, E. M. (2015). High methane emissions dominated annual greenhouse gas balances 30 years after bog rewetting. *Biogeosciences*, 12, 4361–4371.
- Vasander, H., Tuittila, E. S., Lode, E., Lundin, L., Ilomets, M., Sallantausta, T., ... Laine, J. (2003). Status and restoration of peatlands in northern Europe. *Wetlands Ecology and Management*, 11, 51–63.
- Vitt, D. H. (2006). Functional characteristics and indicators of boreal peatlands. In R. K. Wieder, & D. H. Vitt (Eds.), *Boreal peatland ecosystems, Ecological studies*, Vol. 188 (pp. 9–24). Germany: Heidelberg.
- Von Arnold, K., Nilsson, M., Hanell, B., Weslien, P., & Klemetsson, L. (2005). Fluxes of CO₂, CH₄ and N₂O from drained organic soils in deciduous forests. *Soil Biology and Biochemistry*, 37, 1059–1071.
- Von Arnold, K., Weslien, P., Nilsson, M., Svensson, B. H., & Klemetsson, L. (2005). Fluxes of CO₂, CH₄ and N₂O from drained coniferous forests on organic soils. *Forest Ecology and Management*, 210, 239–254.
- Waddington, J., & Day, S. (2007). Methane emissions from a peatland following restoration. *Journal of Geophysical Research-Biogeosciences*, 112(G3), pp. 11.
- Waddington, J. M., & Roulet, N. T. (2000). Carbon balance of a boreal patterned peatland. *Global Change Biology*, 6, 87–98.
- Waddington, J. M., Roulet, N. T., & Swanson, R. V. (1996). Water table control of CH₄ emission enhancement by vascular plants in boreal peatlands. *Journal of Geophysical Research*, 101(D17), 22775–22785.

- Waddington, J. M., & Roulet, N. T. (1996). Atmosphere-wetland carbon exchanges: Scale dependency of CO₂ and CH₄ exchange on the developmental topography of a peatland. *Global Biogeochemical Cycles*, 10, 233–245.
- Walter, B. P., & Heimann, M. (2000). A process-based, climate-sensitive model to derive methane emissions from natural wetlands: Application to five wetland sites, sensitivity to model parameters, and climate. *Global Biogeochemical Cycles*, 14, 745–765.
- Weltzin, J. F., Bridgham, S. D., Pastor, J., Chen, J. Q., & Harth, C. (2003). Potential effects of global warming and drying on peatland plant community composition. *Global Change Biology*, 9, 141–151.
- Whalen, S. C. (2005). Biogeochemistry of methane exchange between natural wetlands and the atmosphere. *Environmental Engineering Science*, 22(1), 73–92.
- White, J. R., Shannon, R. D., Weltzin, J. F., Pastor, J., & Bridgham, S. D. (2008). Effects of soil warming and drying on methane cycling in a northern peatland mesocosm study. *Journal of Geophysical Research*, 113, G00A06.
- Wille, C., Kutzbach, L., Sachs, T., Wagner, D., & Pfeiffer, E. M. (2008). Methane emission from Siberian arctic polygonal tundra: Eddy covariance measurements and modeling. *Global Change Biology*, 14, 1395–1408.
- Wilson, D., Farrell, C. A., Muller, C., Hepp, S., & Renou-Wilson, F. (2013). Rewetted industrial cutaway peatlands in western Ireland: A prime location for climate change mitigation? *Mires and Peat*, 11(1), 1–22.
- Worrall, F., Burt, T. P., & Adamson, J. K. (2006). Trends in drought frequency – the fate of Northern Peatlands. *Climatic Change*, 76, 339–359.
- Worrall, F., Chapman, P., Holden, J., Evans, C., Artz, R., Smith, P., & Grayson, R. (2011). A review of current evidence on carbon fluxes and greenhouse gas emissions from UK peatlands. Report to JNCC. Peterborough, No. 442, ISSN 0963 8901. Accessed in June 2014. Retrieved from http://jncc.defra.gov.uk/pdf/jncc442_webFinal.pdf
- Worrall, F., Reed, M., Warburton, J., & Burt, T. (2003). Carbon budget for a British upland peat catchment. *Science of the Total Environment*, 312 (1–3), 133–146.
- Wu, J., & Roulet, N. T. (2014). Climate change reduces the capacity of northern peatlands to absorb the atmospheric carbon dioxide: The different responses of bogs and fens. *Global Biogeochemical Cycles*, 27, 1005–1024.
- Wuebbles, D. J., & Hayhoe, K. (2002). Atmospheric methane and global change. *Earth-Science Reviews*, 57(3), 177–210.
- Yamulki, S., Anderson, R., Peace, A., & Morison, J. I. L. (2013). Soil CO₂ CH₄ and N₂O fluxes from an afforested lowland raised peatbog in Scotland: Implications for drainage and restoration. *Biogeosciences*, 10, 1051–1065.
- Yang, J. S., Liu, J. S., Wang, J. D., Yu, J. B., Sun, Z. G., & Li, X. H. (2006). Emissions of CH₄ and N₂O from a wetland in the Sanjiang Plain. *Journal of Plant Ecology*, 30, 432–440.
- Yavitt, J. B., & Williams, C. J. (2000). Controls on microbial production methane and carbon dioxide in three Sphagnum-dominated peatland ecosystems as revealed by a reciprocal field peat transplant experiment. *Geomicrobiology Journal*, 17, 61–88.
- Yli-Petäys, M., Laine, J., Vasander, H., & Tuittila, E. S. (2007). Carbon gas exchange of a re-vegetated cut-away peatland five decades after abandonment. *Boreal Environmental Research*, 12, 177–190.
- Yrjölä, K., Tuomivirta, T., Juottonen, H., Putkinen, A., Lappi, K., Tuittila, E. S., ... Fritze, H. (2011). CH₄ production and oxidation processes in a boreal fen ecosystem after long-term water table drawdown. *Global Change Biology*, 17, 1311–1320.
- Zhuang, Q. L., Melillo, J. M., Sarofim, M. C., Kicklighter, D. W., McGuire, A. D., Felzer, B. S., ... Hu, S. M. (2006). CO₂ and CH₄ exchanges between land ecosystems and the atmosphere in northern high latitudes over the 21st century. *Geophysical Research Letter*, 33, 1–5.

How to cite this article: Abdalla, M., Hastings, A., Truu, J., Espenberg, M., Mander, Ü. and Smith, P. (2016), Emissions of methane from northern peatlands: A review of management impacts and implications for future management options. *Ecology and Evolution*, 6: 7080–7102. doi: 10.1002/ece3.2469